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VOLUME 35 SEPTEMBER, 1961 NUMBER 5

MIDDLE ORDOVICIAN PLIOMERIDAE (TRILOBITA) FROM NEVADA, NEW YORK, QUEBEC, NEWFOUNDLAND[1]

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ABSTRACT—The original material of three type species is described, and additional specimens belonging to these three genera including some of *Ectenonotus* like the type but from Nevada, and another species from Newfoundland; some of *Pseudomera* like the type but from Nevada, and a new species from Newfoundland; some of *Pliomerops* from New York State. The genus *Pliomera* is briefly discussed, and the new genus *Colobinion* proposed for a Newfoundland species which may be allied to *Pseudocybele*. Special attention is paid to ventral sutures and the hypostome. It is suggested that the *Pilekia* group and *Diaphanometopus* do not belong in Pliomeridae, and a new diagnosis of the family given. The remarkable similarity between pliomerid species in the early Middle Ordovician of Nevada and Newfoundland supports the correlation based on brachiopods proposed by Cooper.

INTRODUCTION AND ACKNOWLEDGMENTS

AT INTERVALS during the past six years I have collected material of pliomerid trilobites in Nevada and Newfoundland, and examined relevant collections at the Geological Survey of Canada and in the U. S. National Museum. The account of the Pliomeridae in the "Treatise on Invertebrate Paleontology" (ed. Moore, 1959) reveals the inadequacy of published information on certain type species, and the characterisation of the family does not include features that I consider diagnostic. A re-study of all pliomerid genera is not attempted here, but the type and additional material of three species described more than 100 years ago by E. Billings is redescribed. The three genera based on these species are typical pliomerids, though one of them, *Ectenonotus*, was not placed in any family in the "Treatise." The type genus *Pliomera* is briefly characterised, and a new genus erected on material from western Newfoundland. Particular attention is given to ventral cephalic sutures and the hypostome, about which little information was available previously. The revised diagnosis of Pliomeridae is based on this new knowledge and on that of other species in which the exoskeleton is adequately known. The use of subfamilial divisions seems unwarranted at present.

The species described here are from Nevada, Quebec and Western Newfoundland, and all are of early Middle Ordovician age. The similarity between certain Ordovician trilobite and brachiopod faunas of Nevada and Newfoundland has been mentioned by several authors. The illustrations given here underline this similarity, and offer strong support for Cooper's correlation

[1] A part of the cost of the plates in this paper was borne by the author.

(1956) of the upper Pogonip (Antelope Valley limestone) with the Table Head series.

Several of the specimens described here are from a large white limestone boulder in the Cow Head group conglomerate at Lower Head (Kindle and Whittington, 1958, p. 334–335, text-fig. 8). The arguments for the probable age of the fauna from this boulder being Whiterock stage are not repeated here, but the presence of *Pseudomera* and *Ectenonotus* seems to support this view.

In 1954 I collected from the Pogonip group in Nevada under the guidance of Dr. G. Arthur Cooper; a grant from the Shaler Memorial Fund, Harvard University, supported this work. In the same year I visited the Geological Survey of Canada, Ottawa, and photographed the types of trilobites from Newfoundland described by Billings. I am indebted to Dr. H. Frebold for permission to do this work, and to the Harvard Foundation for Advanced Study and Research for funds to undertake it. Studies in Newfoundland are being carried on by Dr. Cecil H. Kindle and me under National Science Foundation grant G 4189. Collections from Lower Head have been made in earlier years by Kindle and more recently by both of us, with the enthusiastic assistance of Mrs. Whittington. Types and figured specimens from our collections are deposited with the Geological Survey of Canada, referred to herein as GSC. Specimens from the U. S. National Museum (abbreviated hereafter as USNM) have been loaned by Dr. G. Arthur Cooper, and from the Peabody Museum, Yale University (abbreviated hereafter as YPM) by Professor Karl M. Waagé. MCZ denotes collections in Museum of Comparative Zoology. Miss Susan Fenollosa prepared the enlargements from my negatives, and Miss Margaret Estey the text-figures.

SYSTEMATIC PALAEONTOLOGY

Family PLIOMERIDAE Raymond, 1913

Diagnosis.—The straight-sided glabella may expand forward slightly, be subparallel-sided, or narrow forward. Occipital furrow has a forward curve in the midpart, so that the occipital ring is narrowest (exs.) behind lateral lobe 1p. Three pairs of lateral glabellar furrows (two in *Pliomerella*), 3p situated far forward on the side or running in from the preglabellar furrow, supplementary furrows (4p ?) rarely developed. There may be a median pit in the preglabellar furrow; no preglabellar field. Posterolateral margins of eye lobe outlined by deep furrow, this furrow continuing forward on inner margin of eye ridge; posteriorly furrow may be continued along line of posterior branch of suture. Anterior branch of suture runs forward and slightly inward on to anterior border of cheek, then inward along the dorsal side of the cephalic border to meet the rostral suture; latter of length (tr.) approximately one-half to one-quarter maximum width of glabella. Connective sutures converge back to define a rostral plate which is narrowest posteriorly, and may be termed steno-ptychopariid in type (Jaanusson, 1956, p. 37). Posterior branch of suture runs outward in curve convex forward and crosses

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EXPLANATION OF PLATE 99

FIGS. *1–4,6–9*—*Ectenonotus westoni* (Billings, 1865), Mystic conglomerate, Range 6, originals of figs. *1–3,6*, from lot 20, originals of figs. *4,7–9*, from lot 21, north of Mystic, Stanbridge Township, Quebec. *1*, lectotype, cranidium, GSC 824a, original of Billings, 1865, fig. 307a, dorsal view, ×2. *2,3,6*, pygidium GSC 824h, original of Billings, 1865, fig. 307b, dorsal, left lateral, posterior views, ×2. *4,7–9*, cephalon and 7 thoracic segments, USNM 138432, anterior, dorsal, left lateral, ventral views, ×2.

5,10–15—*Ectenonotus* cf. *westoni* (Billings, 1865), *Orthidiella* zone, Antelope Valley limestone, upper Pogonip group, White Rock Canyon, Monitor Range, Eureka Co., Nevada. *5*, incomplete cranidium, MCZ 5673b, anterolateral view showing deep preglabellar furrow, ×2. *10,12*, parts of *13* thoracic segments and pygidium, MCZ 5673c, right lateral, dorsal views, ×2. *11,14,15*, cranidium, MCZ 5673a, anterior, left lateral, dorsal views, ×4½. *13*, parts of 13 thoracic segments, dorsal view, ×2.

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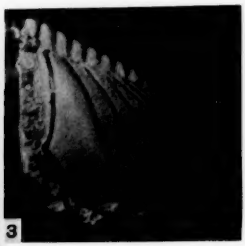
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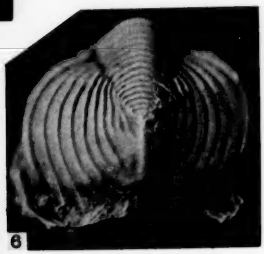
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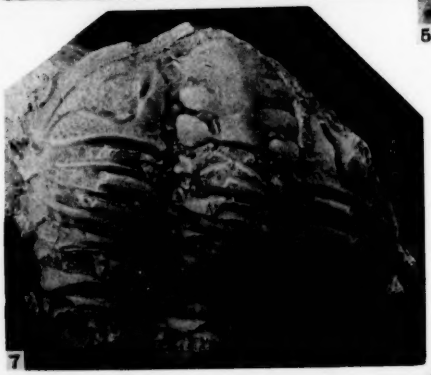
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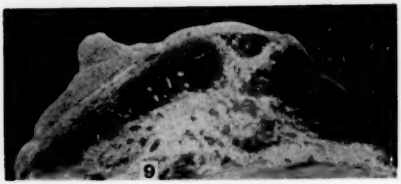
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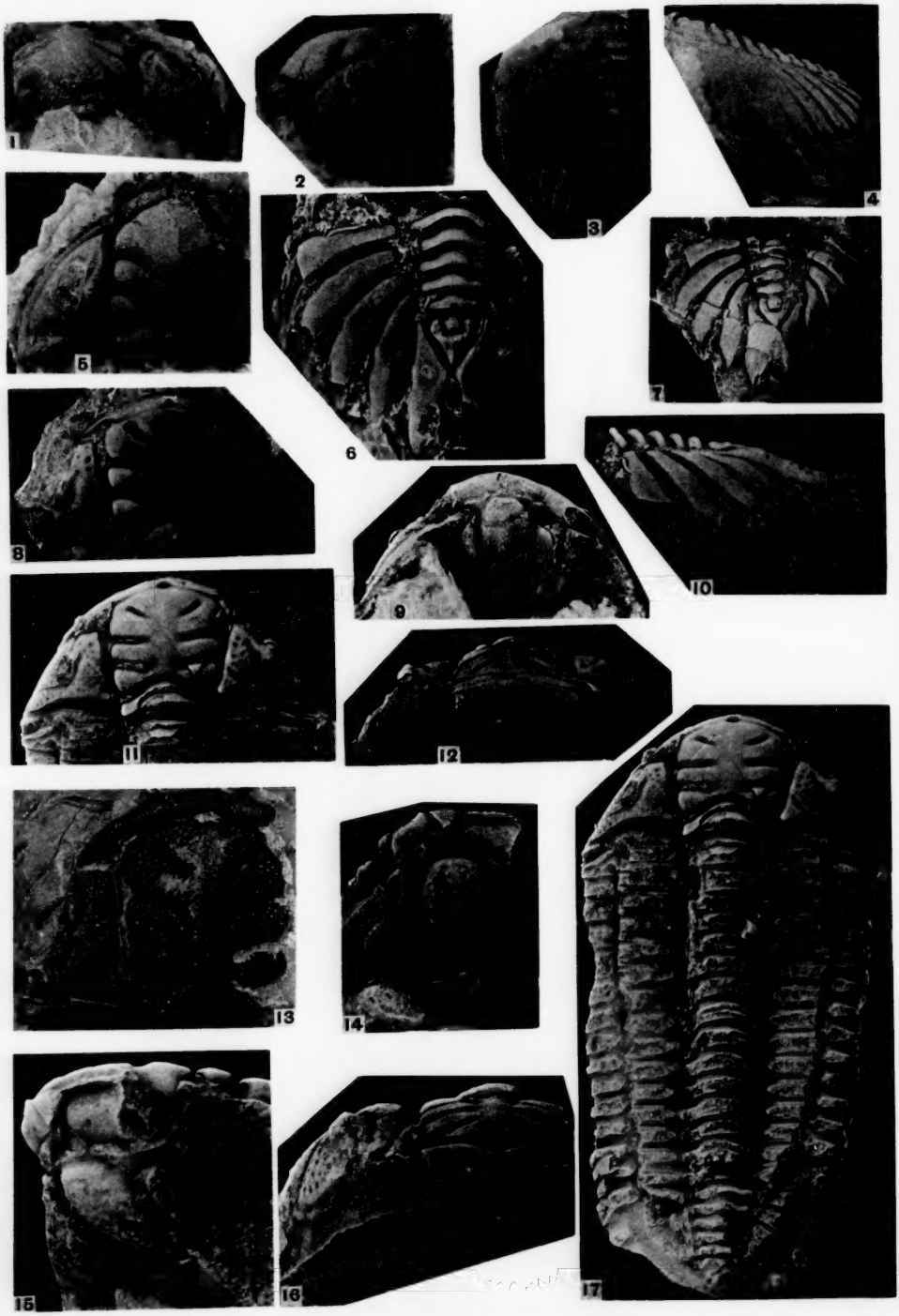
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genal angle, latter rounded or may bear a small fixigenal spine. Hypostomal suture runs along posterior edge of rostral plate and adjacent edges of doublure of free cheeks. Hypostome with convex middle body which is widest in line with the anterior wings and narrows backward, posterior lobe a small crescentic part of this body; lateral and posterior borders broad, may bear spines; large anterior wing, directed upward, rests against side of anterior pit.

Thorax of 12–18 segments, deep pleural furrow close to anterior margin of pleura, posterior band thus broad, convex; pleura may be flexed down sharply at fulcrum, outer part may be broad (exs.) and faceted or a narrow spine. Axis of pygidium of four or more rings and a terminal portion of varying length, pleural regions divided by deep furrows into broad ribs directed progressively more strongly backward, posterior pair of ribs embracing terminal part of axis and in many genera extending side-by-side beyond this terminal part.

External surface granulate, may bear tubercles, cheek inside border furrows pitted in most genera.

Discussion.—Harrington (1957; in Moore, 1959, p. 0439–0445) modified two of the four subfamilies proposed by Hupé (1955, p. 265–267), adopted the other two without change, and added the *Pilekia* group as a subfamily. Jaanusson (in Moore, 1959, p. 0445) added also the monotypic subfamily Diaphanometopinae. It is here suggested that the *Pilekia* group and diaphanometopinids be excluded from the Pliomeridae, and the diagnosis given above embraces the remaining genera included by Harrington, with the addition of *Ectenonotus* and *Colobinion* n.gen.

Pilekiids (cf. Sdzuy, 1955, p. 42–44) have the glabella parallel-sided or narrowing forward, eye lobe situated far forward, eye ridge running inward to the axial furrow, and pleural furrow situated medially. In these respects they are unlike pliomerids. Nothing is known of the pilekiid rostrum, and little of the hypostome (that of *Tesselacauda* Ross, 1951, is not pliomerid-like). It seems best to regard pilekiids either as a separate family, or as a subfamily of Cheiruridae. As Henningsmoen (in Moore, 1959, p. 0431) points out, pilekiids may be the ancestors of some cheirurids.

Diaphanometopus is perhaps more pilekiid than pliomerid in appearance, but its relationships are uncertain. Öpik (1937, p. 115) placed this genus only provisionally in Pliomeridae.

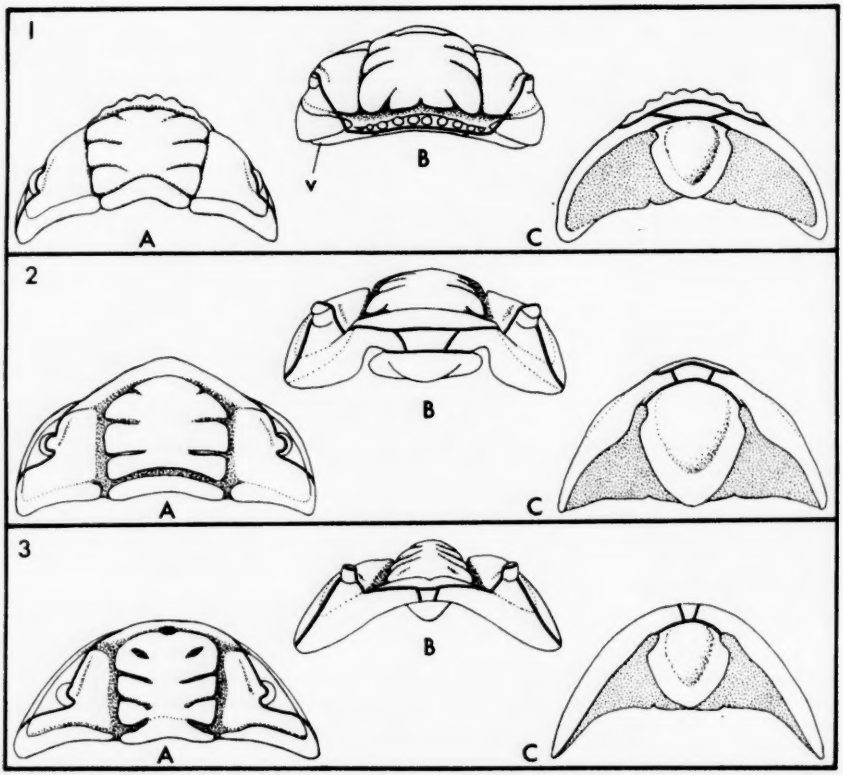
In the Pliomeridae as here conceived, the form of the hypostome, and of the narrow, backwardly-tapering rostral plate, appear to be important diagnostic characters. Rostral plates and hypostomes of four genera are described herein (Text-figs. 1–3,5), and earlier description of others referred to. In addition are the illustrations of Ross (1951,

EXPLANATION OF PLATE 100

FIGS. *1–5*—*Ectenonotus* sp., boulder in conglomerate of upper Cow Head group, Lower Head, Newfoundland. *1,2,5*, incomplete cephalon, GSC 16134, anterior, left lateral, dorsal views, ×6. *3,4*, incomplete pygidium, GSC 16135, dorsal, left lateral views, ×2.

6–8,10—*Pseudomera barrandei* (Billings, 1865), Table Head series, Divisions I, K, L, Point Riche, western Newfoundland, *6,10*, incomplete pygidium, GSC 681a, probable original of Billings, 1865, fig. 277b, dorsal, left lateral views, ×2. *7*, incomplete pygidium, GSC 681, dorsal view, ×2. *8*, lectotype, incomplete cranidium, GSC 681b, original of Billings, 1865, fig. 277a, dorsal view, ×2.

9,11–17—*Pseudomera* cf. *barrandei* (Billings, 1865), sponge beds of upper Pogonip group, *Anomalorthis* zone, Toquima Range, Nevada. *9,11,12,17*, complete exoskeleton, much of exoskeleton stripped away to reveal internal mould, USNM 138433, ventral, dorsal, anterior view of cephalon, dorsal view of entire specimen, ×2. *13*, incomplete cranidium retaining exoskeleton, MCZ 5675, dorsal view, ×2. *14–16*, incomplete cephalon with exoskeleton partly stripped away to reveal internal mould, MCZ 5676, *14*, *16*, ventral and anterior views of cephalon, ×2; *15*, anterolateral view of cephalon showing anterior wing (w) of hypostome projecting dorsally to rest against posterior slope of anterior pit (a), ×2¾.



TEXT-FIGS. *1–3*—Diagrams of the cephala of the type species of three genera of Middle Ordovician pliomerids.

1a–c, *Pliomera*, after Schmidt, 1881; Öpik, 1937; dorsal, anterior and ventral views; v, vincular furrow.

2a–c, *Pliomerops*, after originals of Pl. 101, figs. *15,18,19*, dorsal, anterior and ventral views.

3a–c, *Pseudomera*, after originals of Pl. 100, figs. *8,9,11–17*, dorsal, anterior and ventral views.

pl. 31, figs. 1,2; pl. 33; pl. 34, figs. 24–26), Hintze (1953, pls. 22–25), and accounts of *Placoparia* (Prantl and Šnajdr, 1957; Whittington, in Whittard, 1958, p. 105–106, text-figs. 6a-h). The Pliomeridae are a world-wide group which appears in the Canadian (late Tremadoc and Arenig), is varied in the Middle Ordovician (i.e. Whiterock to Porterfield or Llanvirn to early Caradoc, and one genus persists into the Upper Ordovician (Kielan, 1959).

In diagnosing particular genera in the following pages characters included in the family diagnosis are not repeated.

Genus *Ectenonotus* Raymond, 1920

Type species (by original designation)—*Amphion westoni* Billings, 1865.

Discussion.—Diagnostic of *Ectenonotus* (Text-fig. 4) is the broad, inverted "V"-shaped outline of the anterior margin of the glabella and the sub-parallel margin of the cranidium, the broad preglabellar furrow which is trench-like distally, combined with the positions of the glabellar furrows. The eye lobe is situated far back and relatively close to the glabella. The doublure is broad (sag. and exs.) anteriorly, exceptionally so for a pliomerid. The pygidium is unique

among pliomerids in the number of axial rings and pleural furrows. It is superficially like that of encrinurids, but the eleven pleural furrows commence opposite successive ring furrows, which is not the case in *Encrinurus* or *Cybele* and their allies.

Species of the genus occur in the lowest zone of the type Whiterock stage, earliest Middle Ordovician, of Nevada, at a similar horizon at other localities in Nevada and adjacent California, and in boulders of similar age in conglomerates in Newfoundland and Quebec.

Ectenonotus westoni (Billings, 1865)
Pl. 99, figs. 1–4, 6–9; Text-fig. 4

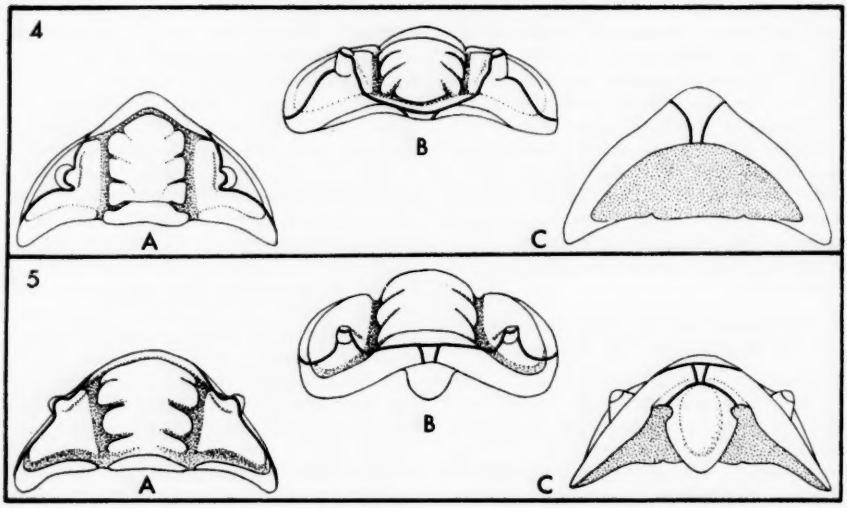
Lectotype (here selected).—GSC 824a, incomplete cranidium, some exoskeleton adhering to the internal mould, original of Billings, 1865, p. 321, fig. 307a, from Mystic conglomerate, Range 6, lot 20, north of Mystic, Stanbridge township, Quebec. Cooper (1956, p. 31) considers the youngest boulders in this conglomerate to be Whiterock in age.

Other material.—GSC 824h, pygidium, original of Billings, 1865, p. 321, fig. 307b; USNM 14706, two incomplete cranidia, counterpart moulds of one pygidium; USNM 138432, cephalon and part of thorax, pygidium; all from same horizon and locality, except USNM 138432 is from lot 21.

Description.—Glabella (Pl. 99, fig. 1) with three lateral glabellar lobes of subequal size, lateral furrow 3p commencing at the anterior margin a short distance inward from the anterolateral corner of the glabella, and directed inward at a more acute angle to the sagittal line than lateral furrows 2p and 1p. Lateral furrow 3p shallow adjacent to preglabellar furrow, deepening rapidly inward, furrows 2p and 1p deep adjacent to axial furrows. Occipital ring narrow (exs.) behind posterior lateral glabellar lobe, small median tubercle. Preglabellar furrow broad, with vertical walls, shallower medially than laterally where it descends as a deep trench to its intersection with the axial furrow. The anterior pit is situated at this intersection. Anterior border flat on upper surface (which is level with anterior part of glabella), prow-shaped in dorsal view, anterior surface descends vertically and curves under into the doublure. Large, high eye lobe situated far back (mid-point in same transverse line as distal end of lateral furrow 1p) and close to glabella, broad, deep palpebral furrow continued forward on inner side of low eye ridge; eye ridge and furrow die out on anterior part of fixed cheek. Posterior border narrow, high, widening distally, posterior border furrow deep. Anterior border descends steeply outward in front of anterior part of fixed cheek, anterolaterally and laterally border widens, slopes steeply outward, and is defined by a broad, shallow border furrow. Genal angle rounded. Distal edge of border laterally and anterolaterally sharp, doublure sloping outward and downward to this edge; doublure widest anteriorly, where edge of border is rounded (Pl. 99, fig. 9). Anterior branch of suture runs straight forward and slightly inward across border furrow and on to upper surface of border, where it curves sharply and runs inward close to the outer edge of the border. The two branches merge with the rostral suture, the latter obliquely angulate at the mid-line. Connective suture commencing at a point on the border in line (exs.) with the inner ends of the lateral glabellar furrows (Pl. 99, fig. 4), running across the doublure in a curve concave outward. Rostral plate narrowest at posterior margin. Hypostome unknown. Posterior branch of suture runs outward and back to genal angle in a curve convex forward, and lies at the bottom of a furrow (Pl. 102, figs. 7,8).

Thoracic pleurae having a deep pleural furrow which curves forward and outward from the axial furrow, then runs distally outward, dying out on the outer part of the pleurae. Anterior band narrow (exs.), convex, lower than the broad (exs.) convex posterior band; outer parts of pleurae bent down vertically at fulcrum, broad (exs.) and faceted.

Pygidium triangular in outline, height almost equal to length (sag.), pleural regions strongly convex, distal parts slope inwards. Axis tapering evenly backward, divided into 15 or 16 rings and a small terminal piece, narrow post-axial ridge runs down vertical posterior slope. Eleven deep pleural furrows curve outward and backward, the last three defining narrow convex ribs that run back parallel to the axis but do not reach the post-axial ridge. Rib between first and second



TEXT-FIGS. *4,5*—Diagrams of the cephala of the type species of two genera of Middle Ordovician pliomerids.

4a–c, Ectenonotus, after originals of Pl. 99, figs. *1,4,7–9*, dorsal, anterior and ventral views; hypostome unknown.

5a–c, Colobinion n. gen., after originals of Pl. 102, figs. *1–3,6,9*, dorsal, anterior and ventral views.

pleural furrows widens (exs.) rapidly distally and is faceted, succeeding ribs narrower, the first four or five ending in blunt free points.

External surface inadequately known, scattered small tubercles on glabella, cheek inside border furrows bearing deep pits; doublure of cephalon granulate.

Ectenonotus cf. *westoni* (Billings, 1865)
Pl. 99, figs. 5,10–15

Material.—MCZ 5673, incomplete cranidia, parts of thorax and pygidia, all from *Orthidiella* zone of Antelope Valley limestone (upper Pogonip group), Whiterock stage, White Rock Canyon, Monitor Range, Eureka Co., Nevada (cf. Nolan, Merriam and Williams, 1956, p. 29).

Discussion.—Species of *Ectenonotus* have been recorded from the upper Pogonip in southwestern Nevada (Holliday, 1942, p. 476–477, pl. 73, figs. 1–3; pl. 74, figs. 1,2,8–10) and adjacent California (Langenheim *et al.*, 1956, p. 2089). The two species of "*Encrinurus*" described by Phleger (1933) from the Mazourka formation, upper Pogonip, may also belong in *Ectenonotus* as Cooper (1956, p. 129) believes.

The present material is extremely like that from Quebec, but the samples from each locality are insufficient to show whether or not there are two or one species. The material of Holliday is too fragmentary and poorly preserved to be useful in comparisons. The small cranidium is typical, the outline of the anterior margin prow-shaped, the preglabellar furrow shallow medially. The large fragmentary cranidium (Pl. 99, fig. 5) shows that the outer part of the preglabellar furrow is a deep, vertical-walled trench, and that the external surface is tuberculate, the area between the tubercles finely granulate. Similar tubercles and granules occur between the large pits in the cheek.

Thorax of at least 13 segments. Pleural furrow curving outward and forward from axial furrow, then running directly outward. Smaller pygidium exhibiting 12 axial rings and terminal portion, eleven pleural furrows, the last two faint. A larger incomplete

pygidium, about the same size as that of the type species from Quebec (Pl. 99, figs. 2,3,6), shows at least 14 axial rings.

Ectenonotus sp.
Pl. 100, figs. 1–5

Material.—GSC 16134, an incomplete cephalon, GSC 16135, a fragment of a pygidium, from boulder in conglomerate of upper Cow Head group, Whiterock stage, Lower Head, Newfoundland.

Discussion.—Cephalon is smaller than that of the Quebec or Nevada material available to me, but the glabella displays the typical outline (the anterior margin a broad, inverted "V") and lobation, and a small median occipital tubercle; lateral glabellar furrow 1p is shorter and shallower than that of the type species. Unfortunately the anterior cephalic border is missing, but the position of the eye lobe, course of the two branches of the suture, and form of the cheek are like those of the type species. The axial rings, pleural furrows and ribs of the pygidium are likewise typical.

Genus *Pseudomera* Holliday, 1942
Text-fig. 3

Type species (by original designation).—*Amphion barrandei* Billings, 1865.

Diagnosis.—Glabella forwardly expanding, lateral furrow 3p commencing immediately inside the outer part of the preglabellar furrow; shallow preglabellar furrow in which there is a median pit, the furrow deepening at the anterolateral angle of the glabella; 15 thoracic segments in one species; axis of pygidium of five rings and a terminal piece in which is impressed a U-shaped furrow (this furrow may connect two pairs of pits and a median posterior depression); five pleural ribs, separated by deep, trench-like pleural furrows, are extended to almost an equal length (tr.) by pleural spines.

Discussion.—*Pseudomera* cf. *barrandei* is recorded and briefly described by Hintze (1953, p. 21,221–222) from zones M and N of the upper Pogonip group. *Pseudomera* cf. *insolita* (Poulsen) of Hintze (1953, pl. 23, figs. 5–13, p. 222–223) seems not to be a species of *Pseudomera*—the outline of the glabella is quite different, there is a deep, broad preglabellar furrow, the borders of the hypostome are broader and bear short spines, and the terminal portion of the pygidial axis lacks the U-shaped furrow. This species resembles the types of *Hintzeia* (*H. aemula*, see Hintze, 1953, pl. 22, figs. 9,13–17, p. 206–207) and *Kanoshia* (*K. kanoshensis*, see Hintze, 1953, pl. 23, figs. 1–4, p. 223). These two genera were proposed by Harrington (1957) and seem to be similar to each other. *Pseudomera* is so far known with certainty only from beds of the upper Pogonip group and Table Head series, of the Whiterock stage.

Pliomerops canadensis (Billings, 1859), type species of *Pliomerops*, is based on a fragmentary cranidium (Pl. 101, fig. 11) and isolated pygidia (Pl. 101, figs. 10,12,13,16; the original of figs. 12,16, illustrated by Twenhofel, 1938, pl. 11, fig. 18) from the Mingan formation, Marmor stage, Mingan Islands, Quebec. More complete specimens from Tennessee have recently been illustrated by Cooper (1953, pl. 10, figs. 5–10). *Pliomerops* (Text-fig. 2) is similar to *Pseudomera*, differing in the absence of a median pit in the preglabellar furrow, the shallow lateral glabellar furrow 3p that commences in the preglabellar furrow, the more rounded outline of the anterior margin of the glabella, the presence of 18 thoracic segments, and the absence of pits or a U-shaped furrow in the triangular terminal piece of the pygidial axis. An enrolled specimen in the U. S. National Museum (Pl. 101, figs. 15,18,19), from the Middle Chazy, Valcour Island, N. Y., shows that the rostral plate is trapezoidal in outline, of width (tr.) at anterior margin about half the maximum width of the glabella; the hypostome is like that of *Pseudomera* but has a relatively wider middle body. A complete specimen, MCZ 5682, from the same horizon and locality, shows the eighteen thoracic segments, as Raymond (1905, pl. 14, fig. 10; 1910, pl. 36, fig. 10) illustrated, though he stated (p. 365 and p. 239 respectively) that there were 19 segments.

Pliomera fischeri (Schmidt, 1881, p. 191–195, pl. 13, figs. 1–8; Öpik, 1937, p. 116–118, pl. 19, fig. 4; pl. 25, fig. 5; text-fig. 32; this paper, Text-fig. 1), type species of *Pliomera*, from the early Middle Ordovician of the Baltic, differs from *Pliomerops* (Text-fig. 2)

mainly in the presence of the short median glabellar furrow extending inward from the preglabellar furrow, the less strongly curved outline of the anterior margin of the glabella, and the anterior cranidial border which bears projections. During enrollment the pleural spines of the pygidium fit into the notches separating these projections (as in some species of *Pseudocybele*, Hintze, 1953, p. 216–217) and there is a vincular furrow in the doublure of the lateral border (v in Text-fig. 1) into which the tips of the thoracic pleurae fit. The trapezoidal rostral plate and the hypostome are typically pliomerid. The characters which distinguish *Pliomera* from *Pliomerops* also distinguish it from *Pseudomera* (Text-fig. 3), and in addition *Pliomera* has a relatively wider (tr.) rostral plate and a small, unfurrowed terminal part of the pygidial axis.

Pseudomera barrandei (Billings, 1865)
Pl. 100, figs. 6–8,10

Lectotype (here selected).—GSC 681b, internal mould of incomplete cranidium, original of Billings, 1865, fig. 277a, from Divisions I, K, L (Table Head series), Point Riche, St. Barbe district, Newfoundland.

Other material.—GSC 681c,d, two cranidia, GSC 681, 681a, two pygidia, all from the same horizon and locality as lectotype; GSC 682, 682a,b, three pygidia, from Divisions L, M, N (Table Head series), Table Head, St. Barbe district, Newfoundland.

Description.—Holliday (1942, pl. 73, figs. 8,10) figured casts of the lectotype and of GSC 682 (stated in error to come from Cow Head). The following notes are based on the lectotype and two pygidia from the same locality (GSC 681, 681a), either of which might be the original of Billings' figure 277b (1865, p. 288). I consider GSC 681a (Pl. 100, figs. 6,10) more likely to be this original.

Straight-sided glabella expanding slightly forward, anterior margin a gentle curve. Occipital furrow deep, swings forward medially so that occipital ring is longer sagittally than exsagittally. Lateral furrows 1p and 2p long, deep, similar in direction, the distance (exs.) between the outer ends equal to the distance between 1p and the occipital furrow. Lateral furrow 3p extremely shallow adjacent to outer part of preglabellar furrow, directed inward and backward at about 45° to axis and becoming deep. Broad, shallow depression in frontal glabellar lobe directed sagittally and extending close to anterior margin. Preglabellar furrow shallow medially, deepening outside the projected line of lateral furrow 3p, deep median pit encroaches into the anterior border. Anterior border of cranidium flat, forward sloping, widest (sag.) medially, narrowest (exs.) in front of fixed cheek. Palpebral lobe situated in line with outer end of lateral furrow 1p, shallow palpebral furrow, low eye ridge runs forward and inward beside anterior branch of suture for a short distance. The specimen is an internal mould, but the fixed cheek may be seen to be pitted.

Axis of pygidium composed of 5 rings and a triangular terminal portion, in which latter is impressed a shallow U-shaped furrow. Anterior axial ring curved convexly forward in the median part, succeeding rings progressively less strongly so curved, the fifth straight. Four deep, trench-like pleural furrows separate the five broad, flat-topped pleural ribs which are extended into tapering spines, curved outward and downward and directed progressively more strongly backward, the posterior pair separated by a short median furrow which lies behind the axis. External surface of exoskeleton not preserved so that this description is of the internal mould.

Pseudomera cf. *barrandei* (Billings, 1865)
Pl. 100, figs. 9,11–17

Material.—MCZ 5675–6, USNM 138433, all from the sponge beds of the upper Pogonip group, *Anomalorthis* zone, Whiterock stage, north wall of Ike's Canyon and 1 mile up from mouth, Toquima Range, Roberts Mountains 1° quadrangle, Nevada.

Description.—The internal mould of the cranidium (Pl. 100, fig. 11) cannot be distinguished from the lectotype (Pl. 100, fig. 8), except that it lacks the depression in the frontal glabellar lobe. An incomplete cranidium with the exoskeleton preserved (Pl. 100, fig. 13) shows that on the external surface furrows appear narrower, but similar in position and relative depth. The external surface of the glabella is tuberculate, the cheek pitted, with granules between the pits. Additional specimens figured here show the narrow (tr.), triangular rostral plate, the

outline of which is preserved on an internal mould (Pl. 100, figs. 9,12) and part of which adheres to a second internal mould (Pl. 100, figs. 14–16). The anterior branch of the suture runs inward and forward on to the border, then curves to run along the anterior face of this border to meet the rostral suture (Text-fig. 3). The hypostome has the convex middle body narrowing backward, the lateral and posterior borders broad and flat. In the internal mould (Pl. 100, fig. 14) the lateral border furrow is deeply impressed, especially posteriorly, the macula appears as a small convexity, and the tip of the long, upwardly directed anterior wing may be seen to lie against the inner, distal part of the anterior boss (Pl. 100, fig. 15).

Thorax of 15 segments (cf. Hintze, 1953, p. 221), inner part of pleura with narrow anterior and posterior flanges, between which is a strongly convex rib. At fulcrum this rib continued as a long pleural spine which descends steeply. Pleural furrow lies between rib and anterior flange. Doublure extends in to articulating devices at fulcrum. Pygidium extremely like that from Newfoundland. The original of Plate 100, figure 17, shows the broad doublure extending in to tip of axis. External surface tuberculate except in furrows.

Pseudomera billingsi n.sp.
Pl. 101, figs. 1–9

Holotype.–GSC 16136, internal mould of incomplete cephalon, boulder in conglomerate of upper Cow Head group, Whiterock stage, Lower Head, Newfoundland.

Other Material.—GSC 16137, figured fragmentary cephalon, GSC 16138, figured pygidium; MCZ 5674, two additional incomplete pygidia, an incomplete internal and an incomplete external mould of the cranidium.

Description.—The holotype cephalon (Pl. 101, figs. 4–6) is half the size of the lectotype of *Pseudomera barrandei* (Pl. 100, fig. 8), the second cephalon (Pl. 3, figs. 1–3) somewhat larger. Both (and a larger fragment) differ from *P. barrandei* in that lateral glabellar furrow 3p commences at the outer end of the preglabellar furrow and becomes shallower inward, and in that it is subparallel to furrow 2p, not at an angle to it. The glabella of the holotype is relatively narrower than that of *P. barrandei*, and the outline of the anterior margin is curved more convexly forward; these differences are less evident in the larger cephalon, which is relatively wider. This latter specimen shows the anterior branches of the suture running inward and downward across the steeply sloping anterior border to meet the narrow (tr.) rostral suture; the rostral plate is subtriangular in outline, the connective sutures running in a curve concave outward and approaching closely at the posterior margin. The posterior branch of the suture lies in a shallow groove that curves across the cheek and border to the genal angle (Pl. 101, fig. 5); where it reaches the margin there is a notch in the border, perhaps for the reception of the anterior thoracic pleurae during enrollment. The eye lobe is similarly situated to that of *P. barrandei*, and a low eye ridge runs forward a short distance and dies out. Cheek inside border furrows deeply pitted.

The pygidium believed to belong to this species differs from that of *P. barrandei* mainly in the different shape and curvature of the pleural ribs and spines, as shown in dorsal and lateral aspects (compare Pl. 101, figs. 7,8 with Pl. 100, figs. 6,10). On an internal mould the U-shaped furrow on the terminal part of the axis is a depressed zone joining two pairs of pits and a median posterior depression.

Discussion.—The holotype is little larger than the incomplete cephalon referred to *Ectenonotus* sp. (Pl. 100, figs. 1,2,5), and differs in the forwardly expanding glabella, the direction, length and depth of the lateral glabellar furrows, and the more forward and outward position of the eye lobe.

Colobinion n. gen.
Type species.—*Amphion julius*
Billings, 1865.

Diagnosis.—Glabella forwardly-expanding, lateral lobe 1p much narrower (exs.) than 2p and 3p, the subparallel lateral glabellar furrows of similar length, 3p commencing immediately behind the anterolateral angle of the glabella (Text-fig. 5). Eye lobe situated opposite lateral glabellar lobe 3p, a short distance out from the axial furrow. Thorax of fifteen or more segments. Pygidium displaying eight axial rings and a small posterior portion of the axis, five pleural ribs prolonged by spines which are of

about equal length (tr.) to the ribs.

Discussion.—*Pseudocybele* Ross (1951, p. 137–140, pl. 33, figs. 1–14, pl. 34, figs. 13–17, 21–27; see also Hintze, 1953, pl. 24) has narrow (exs.) lateral glabellar lobes 1p, and it is possible that *Colobinion* n. gen. is derived from it. If so, the glabella has changed from narrowing forward in the Canadian genus *Pseudocybele*, to expanding forward in the Middle Ordovician genus. Characteristic of Middle Ordovician pliomerids is a forwardly-expanding glabella, and this change may have taken place in several lines of descent. The pygidium of *Pseudocybele* (Hintze, 1953, pl. 24, figs. 10,11a-d) exhibits only five axial rings, and the five pleural ribs are not prolonged by spines.

Colobinion julius (Billings, 1865)
Pl. 102; Text-fig. 5

Holotype.—GSC 680, internal mould of incomplete pygidium, original of Billings, 1865, fig. 279, p. 290, from "P, Cow Head," and probably from a boulder in conglomerate of upper Cow Head group, Whiterock stage, Lower Head, Newfoundland.

Other Material.—The originals of Plate 102 figures 1–3,6–17; in addition are cephala, portions of the thorax and incomplete pygidia; all Kindle and Whittington collection from Lower Head; YPM 13050, 22406b,c are cephala with segments articulated, and 22406a, original of Plate 102, figures 4,5, collected C. Schuchert and C. O. Dunbar, from Lower Head.

Description.—Glabella narrowest across occipital ring, widening forward to lateral lobes 3p, width across frontal lobe the same as across lateral lobes 3p. Occipital furrow narrow, deep, running in curve gently convex forward. The three lateral glabellar furrows deepest at axial furrow, shallowing inward, furrow 1p the deepest and extending to about one-third the glabellar width, 2p and 3p of about same length; furrows 1p and 2p transversely directed, 3p directed slightly backward; furrow 1p close to occipital furrow so that length (exs.) of lobe 1p is the same as that of distal part of occipital ring, lobes 2p, 3p and frontal lobe of about same length (exs.), this length more than twice that of lobe 1p. Lateral furrow 3p commences a short distance behind the anterolateral corner of the glabella. Axial furrow deep, broad; preglabellar furrow narrower and shallower, and exhibiting a shallow pit in the midline. Deep anterior pit at junction of axial and preglabellar furrows. Triangular cheek convex, sloping steeply laterally, border furrows broad and deep. Posterior border narrow adjacent to occipital ring, widening outward and continuous with semitubular lateral and anterior borders. Small, high eye lobe situated far outward and forward on cheek, deep palpebral furrow runs forward and inward a short distance and dies out. Visual surface is the highest outer part of the eye lobe, and bears faint facets (Pl. 102, fig. 16); the lower edge is delimited by a faint furrow. The lower, outer

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EXPLANATION OF PLATE 101

FIGS. *1–9*—*Pseudomera billingsi* n. sp., boulder in conglomerate of upper Cow Head group, Lower Head, Newfoundland. *1–3*, incomplete cephalon, GSC 16137, anterior, anteroventral, dorsal view, ×4. *4–6*, holotype, incomplete cephalon, GSC 16136, anterior, right lateral, dorsal views, ×4. *7–9*, pygidium, GSC 16138, left lateral, dorsal, posterior views, ×2.

10–13,16—*Pliomerops canadensis* (Billings, 1859), Mingan formation, Mingan Islands, Quebec. *10,13*, pygidium, GSC 1101d, Little Hammer Island, ? original of Billings, 1859, fig. 12b, dorsal, posterior views, ×2. *11*, lectotype, here selected, GSC 1101, incomplete cranidium, Little Hammer Island, original of Billings, 1859, fig. 12a, dorsal view, ×2. *12,16*, pygidium, GSC 1094a,? original of Billings, 1865, fig. 278, dorsal, posterior views, ×2.

14,17,20—Pliomerid pygidium, boulder in conglomerate of upper Cow Head group, Lower Head, Newfoundland, GSC 16139, dorsal, posterior, left lateral views, ×9.

15,18,19—*Pliomerops canadensis* (Billings, 1859), Middle Chazy limestone, Valcour Island, Lake Champlain, N. Y. Enrolled exoskeleton, USNM 90034, dorsal, anterior, ventral view of cephalon, ×2.

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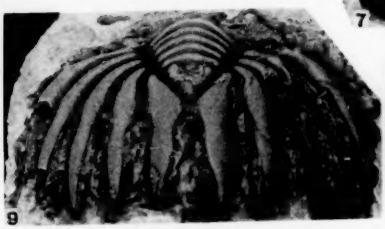
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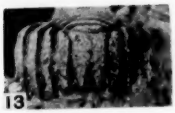
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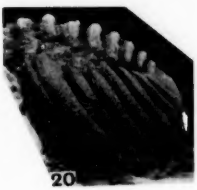
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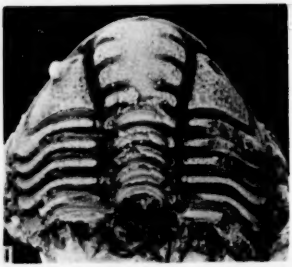
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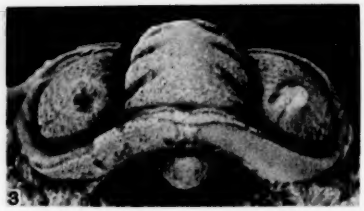
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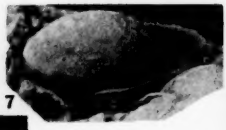
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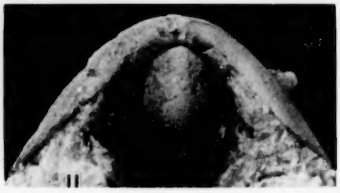
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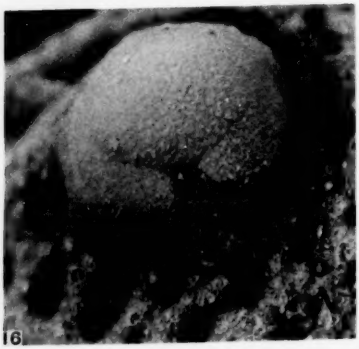
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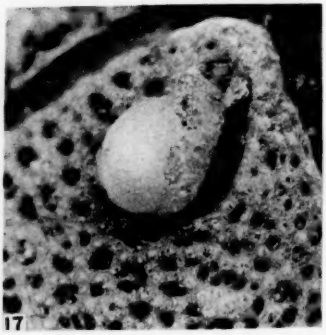
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slope of the lobe below this furrow is divided by a broad depression (d in Pl. 102, fig. 16) into two very slightly convex areas (Pl. 102, figs. 16,17). Anterior branch of suture runs straight forward and slightly inward across border furrow and on to upper surface of border, here it turns to run along outer edge of border to meet the short (tr.) rostral suture. Rostral plate narrows back to half its width at the anterior edge. Posterior branch of suture runs outward and backward in curve convex forward to cross border at genal angle. In ventral aspect doublure is widest anteriorly, narrowing laterally and becoming a sharp edge posterolaterally. Anterior margin of hypostome strongly arcuate in outline, lying medially against the rostral plate and laterally against the doublure of the free cheeks. Anterior border widens distally, small anterior wing directed upward, tip may lie against tip of anterior boss. Middle body oval, strongly convex, small posterior lobe faintly defined. Shoulder obliquely angulate, lateral border narrow, posterior border wider (sag.), tongue-like. Lateral and posterior border furrows deep. External surface of glabella granulate, of middle body of hypostome tuberculate, cheek inside border furrows deeply pitted.

Thorax of at least fifteen segments, as shown by YPM 22406c. Axial ring convex, widening (exs.) distally. Inner part of pleura horizontal, outer of equal width (tr.) and flexed steeply down. Deep pleural furrow runs across inner part immediately inside anterior flange, and dies out beyond fulcrum. Posterior band of inner part of pleura is a strongly convex, transverse ridge which is continuous with rounded posterior edge of outer part of pleura. Latter is broad, rounded at the tip and faceted. No entire exoskeleton has been found, but there are cephala with up to fifteen segments attached. Plate 102, figures 4,5, shows fourteen segments of the same type, slightly beneath which is the disarticulated pygidium, identical with "*Amphion*" *julius* (Pl. 102, fig. 18). I concur with Raymond's (1925, p. 155–156) opinion that these parts belong together. Axis of pygidium tapering evenly to sharp point situated at margin, eight convex rings, a faint ninth ring on the triangular terminal portion. Five convex pleural ribs separated by deep, broad furrows, ribs continued as free spines; first curving gently outward and backward and faceted, successive ribs and spines directed more strongly back, posterior pair embracing posterior part of axis, and spines directed posteriorly. External surface of crests of rings, ribs and spines tuberculate.

Pliomerid pygidium
Pl. 101, figs. 14,17,20

Material.—GSC 16139, a single incomplete pygidium from upper Cow Head group, Whiterock stage, Lower Head, Newfoundland, collected Kindle and Whittington.

Description.—Convex axis tapering rapidly in posterior portion, consisting of articulating half-ring, seven axial rings and a small terminal portion in which is an irregularly

EXPLANATION OF PLATE 102

FIGS. *1–18*—*Colobinion julius* (Billings, 1865), probably all from same boulder in conglomerate of upper Cow Head group, Lower Head, Newfoundland. *1–3,8,11*, GSC 16140, cephalon and 5 thoracic segments, dorsal, left lateral views, ×4½; anterior, anterolateral, ventral views of cephalon, ×6. *4,5*, fourteen thoracic segments and disarticulated pygidium, latex cast from external mould with exoskeleton adhering, YPM 22406a, ×2. *6,7*, hypostome, GSC 16143, external, right lateral views, ×4½.

9,12,16,17, incomplete cephalon, GSC 16141, dorsal and anterior views, ×4½; *16*, lateral view of eye lobe showing posterior branch of suture (p) and depression (d) on outer side, ×30; *17*, dorsal view of eye lobe and adjacent part of cheek, ×15. *10*, incomplete cranidium, GSC 16142, anterolateral view, ×3. *13–15*, incomplete pygidium with part of pleura of last thoracic segment on left side, GSC 16144, posterior, left lateral, dorsal views, ×4½. *18*, holotype, incomplete pygidium, GSC 680, original of Billings, 1865, fig. 279, dorsal view, ×4.

shaped pair of impressions. Pleural region curving steeply downward, subdivided by pleural furrows into a narrow anterior pleural band on the first pleura, followed by seven ribs, the faint last pair embracing the terminal portion of the axis. First rib broadly faceted, at least first three ribs may be extended a short distance as free spines.

No complete exoskeleton of a pliomerid is known from the conglomerate at Lower Head. The association of pygidium with cephalon made for each of the species of *Ectenonotus*, *Pseudomera* and *Colobinion* n. gen. seems probable. No fourth type of cephalon to go with this pygidium is yet known.

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JOURNAL OF PALEONTOLOGY, V. 35, NO. 5, P. 923–926, PL. 103, SEPTEMBER, 1961

AN ICTALURID CATFISH, *ICTALURUS DECORUS* (HAY), FROM THE MIOCENE OF SOUTH DAKOTA

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ABSTRACT—The ictalurid catfish, *Ictalurus decorus* (Hay), is redescribed on the basis of material collected in Bennett County, South Dakota. The species was previously known from a single pectoral spine from the Garvin Gully locality in Texas; the new material includes a well preserved neurocranium and several more spines. A brief review of the fossil catfishes of North America is included.

INTRODUCTION

IN HIS report on the fossil vertebrates of the Garvin Gully fauna of Texas, O. P. Hay (1924, p. 1–2) described and figured the left pectoral spine of a medium-sized Ictalurid catfish. In 1946 Nelson McWhirter collected some catfish remains from the Hemingfordian Flint Hill Fauna of Bennett County, South Dakota. Included in the McWhirter collection are several spines, vertebrae, and a well preserved, although incomplete, neurocranium. This material has been deposited in the collection of the University of Michigan Museum of Paleontology and I am indebted to Dr. Claude W. Hibbard for the opportunity to study and report upon it.

The Flint Hill pectoral spines show close agreement with Hay's figure and description and later work has shown that the Garvin Gully and Flint Hill faunas are both of upper Lower Miocene age (Miller, 1944; Wilson, 1956) I therefore consider the catfish remains of the two faunas to be conspecific and on the basis of the material now available offer the following additions to the brief original description.

Family ICTALURIDAE
Genus ICTALURUS Rafinesque 1820
ICTALURUS DECORUS (Hay)
Pl. 103, figs. 1–7,10,11

Ameiurus ? decorus Hay, 1924, p. 1–2, pl. 1, fig. 1.

Remarks.—The holotype and only specimen known to Hay consisted of a single fragmentary left pectoral spine which was estimated to have had a length of approximately 60 mm. It was collected by Mark Francis from the Garvin Gully locality, 2¼ miles north of Navasota, Texas.

Hay referred this species to the genus *Ameiurus* with some reservation possibly because the size of the specimen indicated a fish somewhat larger than the species usually assigned to that genus. Recently, Taylor (1954) has shown that *Ameiurus* is not distinct from *Ictalurus*, and the present form, in fact, supports Taylor's action for it shares characters of both of the nominal genera *Ameiurus* and *Ictalurus*.

Referred materials.—University of Michigan Museum of Paleontology (UMMP) 26595, neurocranium with attached proatlas centrum and associated miscellaneous fragments. UMMP 32420, a fragmentary hyomandibular. UMMP 32419, two fragmentary right pectoral spines. UMMP 32436, three right and one left pectoral spines, one pectoral spine fragment, one dorsal spine (incomplete), one humeral process of a left cleithrum, one weberian centrum.

Horizon and locality of referred materials.—Flint Hill Fauna, Hemingfordian (upper Lower Miocene). Collected by Nelson McWhirter on the Jim Ross Ranch, west of Martin, South Dakota, July, 1946.

Description.—The neurocranium is somewhat crushed but only slightly distorted. The ethmoids, prefrontals, vomer, and posttemporals are missing but otherwise it is in good condition and most of the sutures and foramina are discernable. In proportions this skull agrees rather well with that of *Ictalurus punctatus* Rafinesque, as will be seen from the measurements given in Table 1 and there can be little doubt that it belongs to the family Ictaluridae as currently understood.

The general arrangement of the bones of the two skulls is nearly identical. Each has a single fossa on the ventral side of the proatlas centrum although that centrum is partially detached from the rest of the

TABLE 1—SKULL MEASUREMENTS OF *Ictalurus decorus* AND *Ictalurus punctatus*
(All measurements in millimeters)

Measurement	*Ictalurus decorus* UMMP 26595	*Ictalurus punctatus* UMMZ 169030-1
Length from tip of supraoccipital spine to anterior end of frontal	96.0	84.2
Width between extremities of anterior edge of pterotic bones	46.5	38.5
Least interorbital width	21.5	20.1
Width at anterior end of frontals	ca. 28	24.8
Length of supraoccipital spine	19.1	20.2
Width of supraoccipital spine at base	11.2	7.0
Depth at middle of orbit	15.6	17.0
Length of posterior dorsal foramen	23.4	21.0
Length of anterior dorsal foramen	21.2	17.2
Length of left hyomandibular articulating socket	25.3	16.3
Least width of parasphenoid	6.9	5.3

basioccipital bone in the fossil; rigidly ankylosed in the recent species. There appear to be substantial differences in the sculpturing of the dorsal surface of the supraoccipital spine (pl. 103, figs. 1 and 2) but this feature is somewhat variable in living catfishes of this family.

Several fish vertebrae were associated with the neurocranium but I am unable at present to definitely assign them to species. The weberian centrum came from a much smaller individual than did the neurocranium and appears to have a shallower ventral groove than that of most Recent species. I do not feel that much significance should be attached to this as the specimen is somewhat worn.

The humeral spine (pl. 103, fig. 7) is in excellent condition and appears to be complete from its base to its distal tip. It has an overall length of 15.2 mm., and is 7.5 mm. wide at its base and has a maximum thickness of 3.5 mm. The sculpturing on its lateral surface (also variable in Recent species) is similar to that of *Ictalurus punctatus* and consists of longitudinal grooves and ridges near the distal end and pits near the basal end.

The dorsal spine is also from a small individual. Its tip is missing; the remaining section is 13.0 mm. long. The structure of the dorsal spine is not known to be diagnostic in this family.

The single associated hyomandibular fragment (UMMP 32420) is very incomplete. The opercular articulation facet remains but there are no other intact margins on the bone. It appears to have been relatively thicker than the corresponding bone in Recent species but this is not reflected in the articulation socket on the neurocranium.

Six fairly complete pectoral spines (pl. 103, figs. 1–6) show relatively little variation. Measurements made according to the method of Hubbs & Hibbard (1951) are presented in Table 2. One spine (number 3 in the table and pl. 103, fig. 3) has definite regular anterior dentations. These are less definite or wanting in other spines and were also lacking in the holotype. This however, is probably the result of wear or age difference for the spines agree in other respects. The shaft is curved backward and is flattened in cross section. Both the upper and lower surfaces bear fine longitudinal striations. The posterior dentations which lie in the posterior groove (terminology after Hubbs & Hibbard, *op. cit.*) and extend but slightly beyond the margins of the posterior groove. Viewed from above they are almost obsolescent, being much less prominent than in a Recent *Ictalurus punctatus* of comparable size. In this respect the fossil seems to be more nearly allied to the bullheads (that section of the genus formerly known as *Ameiurus*) than to the larger channel catfishes (*Ictalurus* s.s.).

DISCUSSION

The North American freshwater catfish family has a fossil record extending from the Eocene to Recent. The rather heavy bones and rugged, well consolidated neurocranium contribute to the chances for preservation and its representatives inhabit a large variety of habitats and often become ex-

TABLE 2—MEASUREMENTS OF SIX PECTORAL SPINES OF *Ictalurus decorus* (HAY)
(Terminology and methods of measuring follows Hubbs & Hibbard, 1951.
All measurements in millimeters)

Measurement	UMMP 32436				UMMP 32419	
	1	2	3	4	5	6
Greatest spine length	18.20	17.52	23.48	26.62	15.28	14.62
Distance between margins of dorsal and anterial processes	8.60	—	11.28	—	4.79	—
Length of dorsal process	5.61	6.18	7.52	6.28	3.60	5.30
Elevation of dorsal process above base of spine	2.51	3.19	3.50	2.90	1.39	2.11
Width of dorsal process to nearest point of rim of central articulating process	3.02	3.83	5.10	4.08	2.06	3.09
Height of anterior process above dorsal base of central articulating process	4.83	—	5.75	—	2.32	—
Maximum width of proximal artic. surface	1.70	—	3.10	—	.99	—
Length of proximal artic. surface	1.40	—	3.19	—	1.09	—
Distance between margins of anterior process and basal process	—	—	6.68	—	2.72	—
Width of anterior fossa	1.77	1.36	1.58	1.99	0.76	1.18
Width of spine	3.18	3.67	4.45	4.21	1.63	2.51
Height of spine	2.42	2.09	2.59	2.82	1.48	2.00
Length of posterior fossa	2.10	2.13	3.52	2.49	1.19	1.99
Width of posterior fossa	1.10	1.00	1.96	1.37	0.51	0.92
Length of central artic. surface	2.30	2.49	3.71	2.65	1.48	2.48
Width of central artic. surface	—	1.68	2.50	1.90	1.01	1.49
Length basal recess	—	3.11	5.08	3.91	2.60	2.88
Width basal recess	—	1.80	2.85	2.10	.98	1.69

tremely abundant. Pectoral spines are common in Pleistocene and Pliocene deposits but whole skeletons or even crania are less frequently preserved intact. In many species the structure of the pectoral spine furnishes excellent diagnostic characters although like almost any external part they are subject to individual variation and to variations due to wear, breaking of the tips, sex dimorphism and perhaps other effects of the environment in which they live. Fortunately, they are sometimes found in sufficient numbers so that their variations can be evaluated.

The oldest record of an ictalurid catfish is the specimen described by Eastman (1917) as *Ameiurus primaevus*. This is based on an unlabeled specimen in the United States National Museum but from the nature of the matrix it appeared to have come from the Green River Eocene shales. It is an almost complete skeleton and from Eastman's plate there can be little doubt that it belongs to this family. The chief characters listed by Eastman are the low anal ray count (about 12) and the lack of dentations on the pectoral spines (Eastman, 1917, p. 293–294, pl. 20).

Cope (1891) described two species, *Ameiurus cancellatus* and *A. maconnelli* from the Cypress Hills Oligocene deposits of Saskatchewan. Each of these was based on two vertebrae hence it is difficult to compare them with Recent or other fossil forms. Other catfishes from the Oligocene are in museum collections but have not yet been reported.

Matthews (1918, 1924) listed some undetermined catfish remains from the Snake Creek Miocene fauna. These should be compared with *Ictalurus decorus* (Hay).

Ictalurus lambda Hubbs & Hibbard (1951) is a very large catfish allied to *Ictalurus furcatus* (LeSueur) of the Mississippi valley. It is known from the Ogalalla formation (lower Pliocene). Other records from the Pliocene will be reported upon in a separate paper.

Abundant catfish remains are found in glacial and interglacial deposits of the high plains. *Ictalurus melas* (Rafinesque) and *I. punctatus* (Rafinesque) have been reported

from the Illinoian by Smith (1954, 1958). Leidy (1889) reported *Ameiurus atrarius* (= *Ictalurus nebulosus* (LeSueur)) from a Pleistocene fissure deposit in the limestones of Pennsylvania.

Apparently the family Ictaluridae was well differentiated by the time of its appearance in the Eocene. The fossil record as it stands today gives scant clues as to the time or place of its origin.

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EXPLANATION OF PLATE 103

FIGS. *1–4*—Pectoral spines of *Ictalurus decorus* (Hay). UMMP 32436, *1*, right spine 18.20 mm. long. *2*, right spine 17.52 mm. long. *3*, right spine 23.48 mm. long. *4*, left spine 26.62 mm. long. The upper view of each figure is of the dorsal side, the lower is the posterior face.

5,6—Pectoral spines of *Ictalurus decorus* (Hay). UMMP 32419. *5*, right spine 15.28 mm. long. *6*, right spine 14.62 mm. long.

7—Humeral process of left cleithrum of *Ictalurus decorus* (Hay). UMMP 32436, overall length 15.2 mm.

8,9—Neurocranium of *Ictalurus punctatus* (Rafinesque). UMMZ 169030, overall length 84.2 mm. *8*, ventral view. *9*, dorsal view.

10,11—Neurocranium of *Ictalurus decorus* (Hay). UMMP 26595, overall length 96.0 mm. *10*, ventral view. *11*, dorsal view.

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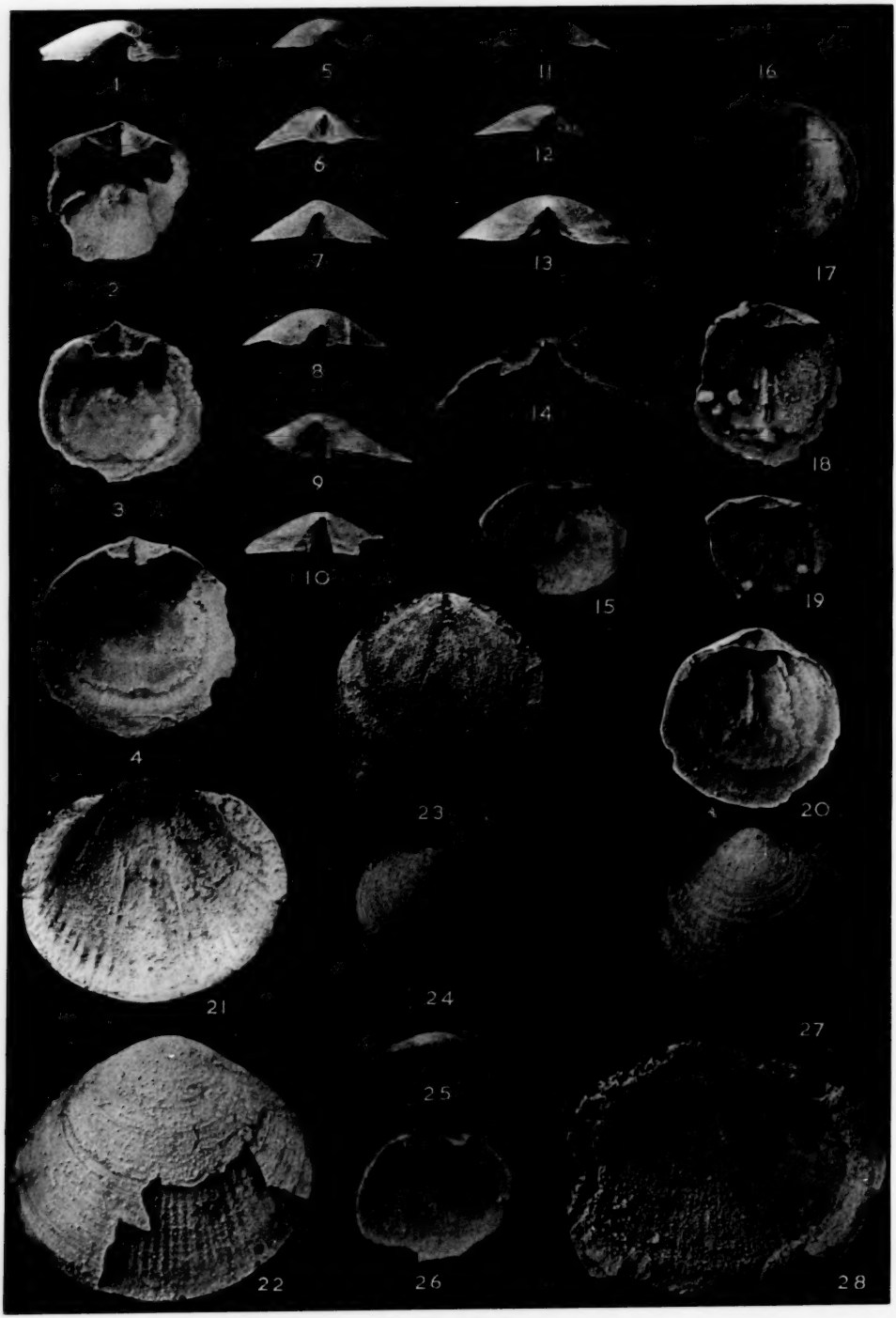
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JOURNAL OF PALEONTOLOGY, V. 35, NO. 5, P. 927–931, PL. 104, SEPTEMBER, 1961

THE INARTICULATE BRACHIOPOD *CURTICIA* WALCOTT

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ABSTRACT—Two species of the Cambrian inarticulate brachiopod *Curticia* are redescribed and illustrated. *C. minuta* Bell is redescribed from etched material and *C. elegantula* Walcott from mechanically prepared material.

INTRODUCTION

THE genus *Curticia* was erected by Walcott (1905, p. 319) for the single species *C. elegantula* Walcott from the Upper Cambrian (Franconian) of Minnesota. This remained the only species in the genus until Bell (1944, p. 145) described *C. minuta* from somewhat older (Dresbachian) rocks in Montana. Walcott and Schuchert (1908, p. 143) erected the family Curticidae for the single genus *Curticia*, and considered that it was a primative obolaceid.

Bell's discovery (1948) that acetic acid could be used to etch inarticulate brachiopods from limestone, and the more recent application of formic acid to the same purpose, have greatly improved the quality of specimens that can be obtained. Excellent

EXPLANATION OF PLATE 104

Repositories: numbers prefixed U.T. Department of Geology, University of Texas; U.S.N.M. United States National Museum.

FIGS. *1–20*—*Curticia minuta* Bell. All specimens from Half Moon Pass, Big Snowy Mountains, Montana, *Crepicephalus* Zone. Horizon numbers are those of Lochman, published in Lochman and Duncan (1944, p. 20). Horizons 9.4 and 9.5 were considered by these authors to be the same. All approximately ×16. *1,2*, posterior and ventral interior view of ventral valve with large triangular, externally strongly concave propareas, U.T. 12385, horizon 9.4. *3*, ventral interior showing muscle scars and pallial marks, U.T. 12384, horizon 9.4. *4*, ventral interior of almost perfect ventral valve showing narrower propareas, U.T. 13286, horizon 9.4. *5–10*, morphological series showing development of pedicle opening. Posterior view of ventral valves. *5*, smallest specimen obtained, foramen an elongate slit, U.T. 12388. *6*, somewhat larger specimen, propareas still united dorsally, U.T. 12389. *7*, early stage in the development of the two discrete propareas, U.T. 12390. *8*, parallel sided pedicle opening produced by continued resorbtion, U.T. 12391. *9*, specimen with somewhat higher propareas, pedicle opening still parallel sided, U.T. 12392. *10*, specimen with triangular pedicle opening, U.T. 12393. All from horizon 9.5. *11*, posterior view of ventral valve. Specimen with propareas strongly marked off from postero-lateral slopes of the shell, U.T. 12394, horizon 9.5. *12*, posterior view of a ventral valve. Specimen with low pseudointerarea, triangular pedicle opening and narrow propareas, U.T. 12395, horizon 9.5. *13*, posterior view of specimen illustrated in fig. 4, U.T. 12386. *14*, posterior view of a ventral valve from a somewhat lower horizon in the *Crepicephalus* zone. Specimen tilted slightly to show the very narrow propareas, U.T. 12396, horizon 9.2. *15*, ventral interior showing straight propareas, U.T. 12383, horizon 9.4. *16,17*, posterior and ventral interior view of ventral valve of specimen with small propareas, U.T. 12387, horizon 9.4. *18,19*, dorsal interiors showing variation in shape of the median plate. *18*, U.T. 12399. *19*, U.T. 12398, both from horizon 9.4. *20*, dorsal inteior showing median plate, propareas and muscle scars, U.T. 12397, horizon 9.5.

21–28—*Curticia elegantula* Walcott. All specimens from the Upper Cambrian "St. Croix Sandstone," Taylors Falls, Chisago County, Minnesota. Walcott locality 82 b. Figs. *21–27* all approximately ×8, Fig. *28* ×10. *21*, dorsal interior, figured Walcott (1912) Pl. 1, fig. 2k, U.S.N.M. 51902l. *22*, ventral exterior exposing inner layers of shell, figured Walcott (1912) Pl. 1, fig. 2c, U.S.N.M. 51902d. *23*, cast of dorsal interior showing anterior muscle scars and median ridge, figured Walcott (1912) Pl. 1, fig. 2l, U.S.N.M. 51902m. *24*, exterior of ventral valve of lectotype, figured Walcott (1912) Pl. 1, fig. 2, U.S.N.M. 51902a. *25*, posterior view of ventral valve of lectotype, pseudointerarea obscured by matrix, figured Walcott (1912) Pl. 1, fig. 2′, U.S.N.M. 51902a. *26*, interior of ventral valve to show narrow propareas, U.T. 123400. *27*, dorsal exterior figured Walcott (1912) Pl. 1, fig. 2j, U.S.N.M. 51902k. *28*, dorsal interior showing anterior muscle scars U.S.N.M. 51902o.

specimens of *C. minuta* from Montana include a number of early growth stages. The Montana specimens are from a slightly higher horizon in the *Crepicephalus* Zone of the Half Moon Pass section than the type material of *C. minuta*. They differ from the types in being somewhat smaller and frequently have larger propareas. However, as little is known about the variation of *C. minuta* from the type locality and our specimens show many resemblances we have referred them to that species.

The acid etching method unfortunately cannot be applied to the *Curticia elegantula* material for the fossils are preserved in medium grained dolomitic sandstone. However, new mechanical preparations of topotype material in the University of Texas Collections and re-examination of Walcott's type specimens in the U. S. National Museum have provided fresh information about the nature of the pedicle opening in this, the type species of the genus.

From additional information about both species the genus can be redefined in rather more detail than has previously been possible. Furthermore, the study of early growth stages requires that the family be transferred from the Obolacea to the Acrotretacea.

Superfamily ACROTRETACEA Schuchert, 1893

[*nom. transl.* Schuchert, 1896 (*ex* Acrotretidae Schuchert, 1893)]

Family CURTICIDAE Walcott and Schuchert, 1908 emended

Ventri-biconvex Acrotretacea in which the early pedicle foramen is enlarged dorsally by resorbtion to produce a triangular pedicle opening that separates two discrete propareas.

Genus CURTICIA Walcott, 1905 emended

Curticia Walcott, 1905, p. 319; 1912, p. 369, pl. 1, figs. 2,2a–21.

Type species *Curticia elegantula* Walcott.

Suboval outline, ventri-biconvex; shell chitinophosphatic, inner layer of lamellae obliquely inclined to shell surface, impunctate; outer surface of shell ornamented by fine concentric growth lines.

Ventral beak small, slightly overhanging the pseudointerarea, posterior slope catacline to apsacline. Pseudointerarea perforated by elongated pedicle foramen in the young forms, subsequent resorption produces open, usually triangular delthyrium bounded laterally by two propareas in adults. Ventral musculature consists of a pair of large cardinal scars on posterolateral slopes and a pair of small scars close to the midline, slightly anterior to cardinals. A pair of pallial sinus trunks diverge anterolaterally from the beak, passing between the cardinal scars and the smaller anterior pair.

Dorsal beak marginal; median triangular plate in front of beak bounded laterally by two narrowly triangular propareas. Low median ridge variably developed. A pair of low ridges may be present diverging anterolaterally from a short distance in front of the beak, and have small anterior muscle scars developed at about the mid-length of the valve on them. Large cardinal scars on the posterolateral slopes of the valve. Pallial markings obscure.

CURTICIA MINUTA Bell
Pl. 104, figs. 1–20

Curticia minuta Bell, 1944, p. 145, pl. 18, figs. 22–31.

Subcircular in outline, greatest width slightly anterior to the middle of the shell. Average adult 1.8–2.0 mm. wide. Biconvex, convexity of the ventral valve considerably greater than that of the dorsal. Both valves ornamented only by fine, irregularly spaced growth lines; surface of valves glossy. Shell chitinophosphatic, thin and laminated; inner lamellae sharply inclined to the surface at their anterior margins and bearing closely spaced radiating ridges; no punctae or pits in any shell layer.

Ventral valve. In lateral profile the anterior slope is very gently convex, maximum convexity in the posterior third of the valve. Beak small, projecting slightly posterior to the commissure; posterior margin beneath the beak concave. In posterior profile the two lateral margins are very gently convex. Beak thickened internally. The pseudointerarea is concave externally and its two outer margins are marked off from the posterolateral flanks of the valve by rather sharp

flexures of the shell. The pseudointerarea has an apical angle of 80°–100°. In the adult it is divided into two propareas by a triangular pedicle opening, and a distinct hemiconical collar or groove links the two propareas at the apex of the opening. The propareas are ornamented parallel to their base by growth lines which are continuous with those in the pedicle collar or groove. The pedicle opening varies considerably in shape (pl. 104, figs. 1,10,13,14,16) in specimens of a similar size; at one extreme it is long and narrow with parallel or even slightly convergent sides, at the other extreme it is broadly triangular. There is a similar large, continuous variation in the shape, size and inclination of the propareas. They range from little more than ridges bounding the pedicle opening (pl. 104, fig. 14) to large triangular plates (pl. 104, fig. 1); they may be nearly co-linear or converge anteriorly towards the midline so that they are strongly concave externally (pl. 104, figs. 3,15 and 17). The muscle scars consist of two pairs, a large pair of cardinal scars on the posterolateral slope immediately lateral to the propareas, and a second pair close to the midline and slightly in front of the anterior margin of the cardinal scars (pl. 104, figs. 2,3 and 17). Two broad pallial sinus trunks run in a slightly curved path anterolaterally from the beak between the cardinal and the smaller pair of muscle scars.

Dorsal beak marginal, greatest height of the valve about one third the length from the beak. Internally there is a small subtriangular plate immediately in front of the beak that may project as a shelf into the valve. Plate lies approximately in the plane of commissure of the valves, has an apical angle of 100° to 130°, and is ornamented by faint growth lines parallel to its base; separated laterally by sharp flexures of the shell from the two anacline, narrowly triangular propareas. Striated propareas raised slightly above general level of posterior margin of valve and may project a short distance into valve cavity, giving the impression of two peglike elevations on the posterior margin of the shell. The median plate and propareas show considerable variation in shape and size (pl. 104, figs. 18–20). A low median ridge is developed. It arises about one fifth the length anterior of the beak and extends forward to about the centre of the valve. Two large cardinal muscle scars are present in the posterolateral area of the valve, immediately in front of the propareas. A second, smaller pair of scars is developed near the center of the valve, close to the midline. These may occur on two low ridges which converge towards the beak (pl. 104, figs. 18 and 19). Pallial markings unknown.

Development of the pedicle opening.—Among the acid residues are a number of juvenile specimens that show clearly the development of the pedicle opening. The smallest specimen, 1.1 mm. wide and 1 mm. long (pl. 104, fig. 5), is similar to an adult except for the pedicle opening. The beak slightly overhangs the small triangular pseudointerarea. The pedicle emerged through an elongated foramen that divides the interarea into two propareas; these however are not discrete, and are joined dorsal to the foramen. Subsequently, this narrow band of shell is resorbed (pl. 104, fig. 6) and the propareas are then separated by an elongated pedicle opening whose lateral margins converge but do not meet dorsally (pl. 104, fig. 7). With continued growth of the animal there is a tendency for the pedicle opening to become more triangular. A morphological series showing this change is illustrated on pl. 104, figs. 5–10. As is apparent from the description of the adults, the final form of the pedicle opening and propareas shows considerable variation, but the condition of joined propareas is a feature only of the young stages. In all adults the connecting shell material dorsal to the foramen is resorbed.

The growth lines on the pedicle groove connecting the two propareas (pl. 104, fig. 2) show that it developed by migration in an anterodorsal direction of the epithelium that secretes it. In this respect it is homologous to the pedicle collar of the articulate brachiopods, which originates in a similar manner (Cf. Williams 1956, p. 255).

Discussion.—This species differs most obviously from *C. elegantula* in its much smaller size and thinner shell. The radial markings on the inner layers of the shell are much less conspicuous in *C. minuta* and the two lateral ridges in the dorsal valve are more faintly developed.

CURTICIA ELEGANTULA Walcott
Pl. 104, figs. 21–28

Curticia elegantula Walcott, 1905, p. 319; 1912, p. 369, pl. 1, figs. 2,2a–21.

Small to medium sized, average width about 5 mm. Shell ventribiconvex, subelliptical in outline, chitinophosphatic, formed of two layers; inner layer of lamellae oblique to the outer surface of the shell. Inner layer of the shell ornamented by fine radial lines, outer layer ornamented only by fine growth lines.

Ventral valve. In lateral profile the anterior slope is gently convex, its highest point about one third the length forward from the beak. Beak small, slightly incurved over the pseudointerarea. Posterior slope catacline to apsacline. Pseudointerarea with an apical angle of about 90°, marked off from the posterolateral slopes of the valve by a shape anteriorly directed flexure of the shell. Pseudointerarea bisected by a broadly triangular pedicle opening. Propareas narrowly triangular, ornamented by growth lines parallel to their base, connected by a thin pedicle groove or collar at their apex (pl. 104 fig. 26). The muscle and pallial marks are not clearly impressed on the valve, but there are indications of a pair of cardinal scars on the posterolateral slopes.

Dorsal valve. In lateral profile fairly evenly convex, convexity slightly greater in the posterior half of the valve. Beak small, projecting a short distance behind the remainder of the posterior margin. No specimens retain perfect dorsal posterior margin; propareas not observed. Internally a median ridge is usually developed extending forward about one third the length of the valve from the beak. It may continue as a much lower ridge into the center of the valve. An additional pair of low ridges normally is developed; they arise a short distance in front of the beak and diverge anterolaterally from the median ridge, making an angle of about 45° with each other. Cardinal muscle scars not observed; pair of elongate scars near the center of the valve, one on each of the lateral ridges.

This species is two or three times as large as *C. minuta* and has a correspondingly thicker shell. The ventral propareas, in as far as they are known, are always relatively smaller than the usual size in *C. minuta*. This difference, however, may well be more apparent than real, because the specimens have to be cleaned mechanically and insufficient information has been obtained to reveal the variation in this character. There will also be a selective tendency for the larger propareas to fracture during the process of cleaning the specimen.

SYSTEMATIC POSITION OF THE FAMILY

The family was initially placed in the Obolacea (Walcott, 1908, p. 143). It was thought at that time that *Curticia* had internal characters similar to *Obolus* and that the pedicle emerged through a simple triangular opening at the posterior margin of the shell. It is easy to understand how the details of the pedicle opening were missed when all the material had to be cleaned mechanically for the excavation of such minute features with a needle presents considerable difficulties. Earlier describers of *Curticia* mistook the outside margins of the pseudointerarea for the edge of the delthyrium; the propareas and pedicle opening actually were still covered by a thin layer of matrix (see pl. 104, fig. 25, Walcott, 1912, pl. 1, figs. 2′,2d, and Bell, 1944, pl. 18, fig. 25).

The musculature in both valves is almost identical with that of the acrotretid species *Linnarssonella girtyi* Walcott and *Apsotreta expansa* Palmer. These two species, which have an external shape and apsacline profile similar to *Curticia*, have so-called "apical pits" (Palmer, 1955, p. 768) situated on either side of the mid-line on the anterior slope of the ventral valve. These muscle scars would appear to correspond to the small pair of anterior scars in the ventral valve of *Curticia*, which are situated in a very similar position. The cardinal scars in the ventral valve are apparently homologous in all three genera. There is a similar close correspondence in the dorsal musculature. The pallial sinus pattern of the ventral valve in *Curticia* is similar to that of many acrotretid genera, and the character of the dorsal posterior margin is typically acrotretid, again showing a particularly close resemblance to that of *Linnarssonella*.

The adult pedicle opening does not resemble that of any described acrotretid genus, but in its early stages of development, when

it is an elongate foramen, there is some measure of similarity.

The close resemblance of so many features leads us to include the family Curticidae in the Acrotretacea.

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One of us (A. J. R.) wishes to express his thanks to Dr. and Mrs. G. A. Cooper for their hospitality, the Geological Society of America for a Project Grant from the Penrose Bequest to defray expenses of work on the inarticulate brachiopods for the Treatise on Invertebrate Paleontology and to Dr. R. C. Moore for his assistance in making his visit to the United States possible.

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DEVONIAN STROMATOPOROIDS FROM THE CANADIAN ROCKY MOUNTAINS

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ABSTRACT—In the carbonate facies of the Fairholme group (Upper and possibly Middle Devonian) stromatoporoids are important rock-formating and reef-bulding organisms. A fauna from these beds and from the overlying Alexo and Palliser formations is described. At the top of the Devonian succession a new species of *Labechia* (*L. palliseri*) occurs. A new genus, *Hammatostroma*, is established for stromatoporoids of the family Clathrodictyidae in which the pillars do not extend directly between the laminae but are bent to form a tangled structure in the interlaminar space. *Hammatostroma albertense* is described as the species typical of this genus. Two new species of *Atelodictyon* (*A. stelliferum*, *A. ordinatum*) and *Trupetostroma* (*T. lecomptei*, *T. tenue*) are described and a new species of the genus *Anostylostroma* (*A. vesiculosum*).

INTRODUCTION

STROMATOPOROIDS are abundant in the carbonate facies of the Devonian rocks of Alberta. In the reefal dolomite beds they appear to be one of the most important rock-forming and frame-building organisms. Unfortunately dolomitization has obliterated the details of the structure of many specimens but at a few localities fossils of this group are well enough preserved for identification. The writer collected stromatoporoids from many Devonian stratigraphic sections during the field seasons of 1954, 1955, and 1956 when he was employed by the Canadian Gulf Oil Co. (which subsequently merged with the British American Oil Co.) in studies of the late Paleozoic stratigraphy of the Canadian Rocky Mountains. Of the many measured sections from which stromatoporoids were collected, only twenty-one yielded well preserved specimens. The localities are plotted on text-fig. 1.

The stromatoporoid fauna is a large one and as many as twenty species seem to be present in the writer's collection. However, those species which are represented by a single poorly preserved specimen have not been described in this paper in the expectation that further collecting will make more and better preserved specimens available. This paper is a progress report on work that continues on the Devonian stromatoporoids of the west.

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STRATIGRAPHY

The Devonian succession in Alberta consists of the Fairholme group overlain by the Alexo formation and the Palliser limestone. The Fairholme group can be divided into a carbonate or reef facies and a shale or basinal facies. The areal extent of these facies in the Rocky Mountains is indicated on the index map (text-fig. 1). The carbonate facies is composed largely of biohermal and biostromal dolomites in the Rocky Mountains but contains much intercalated anhydrite in its extension beneath the plains of southern Alberta. Along much of the boundary between the two facies large masses of porous, unbedded, light grey dolomite record the presence of reefs in the Devonian seas.

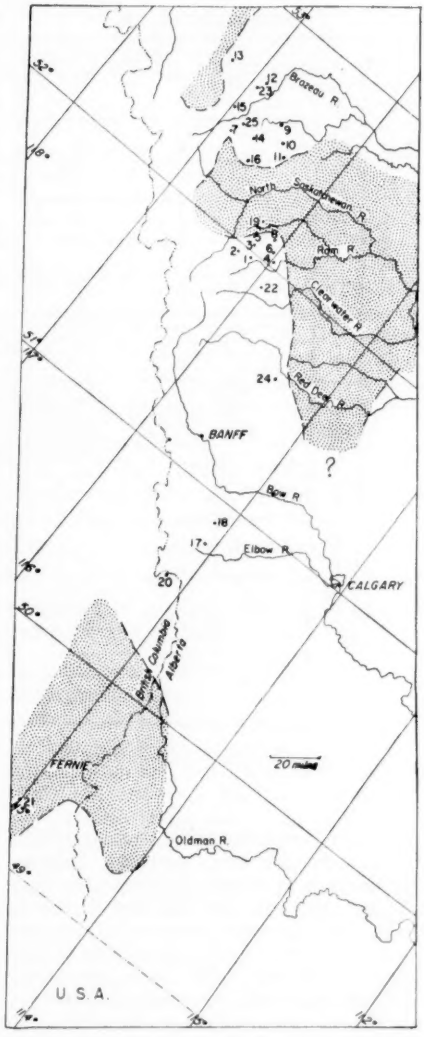
The stratigraphy of the Devonian rocks of Alberta has been described in a series of papers by Belyea and McLaren, and by Taylor (McLaren, 1956; Belyea, 1955, 1957, 1958; McLaren & Belyea, 1957; Taylor, 1957). The stratigraphic relations are sum-

marized in text-fig. 2. The lithologic divisions of the section used by McLaren and Belyea are followed in this paper.

The carbonate facies of the Fairholme group has been divided by McLaren into two formations. The Cairn formation below is composed of dark grey to black, granular dolomite in which stromatoporoids and especially *Amphipora* are abundant but not commonly well preserved. Much of this unit, particularly its upper part, is reefal in structure. It is overlain by the light grey dolomite of the Southesk formation which in many places can be divided into three members. The lowest member called the Peechee is composed of massive, porous, light grey dolomite that is largely unbedded near the boundary of the reefal facies but becomes more bedded and less reefal away from the margin. Although much of this member is obviously organic and perhaps of algal origin, the light grey dolomite contains few recognizable fossils. The only stromatoporoids are found in thin, dark grey dolomite interbeds. The Grotto member is composed of slightly argillaceous, dark grey dolomite with many corals and stromatoporoids. The Arcs member forms the top of the Fairholme group and consists of light grey, bedded dolomite. The Arcs and Grotto members can be recognized as tongues into the basinal facies some distance beyond the abrupt disappearance of the Peechee dolomite.

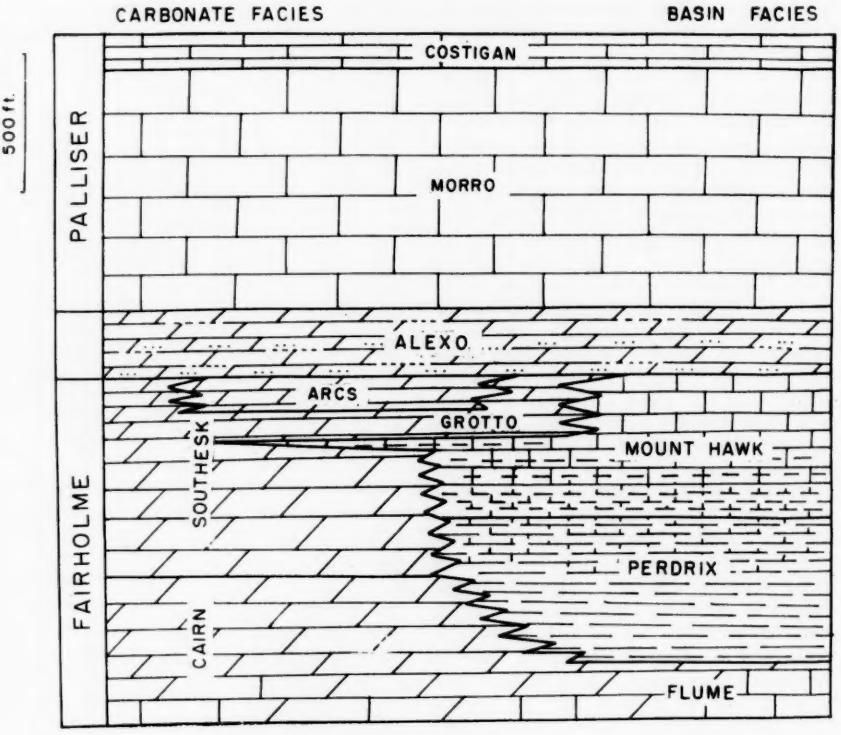
The basinal sequence has been divided into three formations. The Flume formation at the base consists of dark grey, bedded and reefal dolomites not unlike parts of the Cairn formation, and some limestone. The Perdrix is dark grey interbedded calcareous shale and highly argillaceous limestone with very few fossils. The Mount Hawk formation is largely highly argillaceous limestone of light brownish grey color with some nodular calcareous shale. Parts of this formation bear an abundant coral-brachiopod fauna.

Both basinal and carbonate facies are overlain by the Alexo formation of silty limestone, siltstone, breccia, and dolomite. The Palliser limestone which is the topmost unit of the Devonian succession is divided into a lower massive, partly dolomitized Morro member and an upper, thinner, rubbly bedded Costigan member. Most of the fauna of the Palliser limestone has been collected from the Costigan member.



TEXT-FIG. 1—Index map to stromatoporoid localities in the Canadian Rocky Mountains. Numbers refer to localities listed in the Appendix. The extent of the basin facies is indicated by the patterned areas.

The boundary between the Upper and Middle Devonian series in this sequence has



TEXT-FIG. 2—Facies diagram of the Devonian formations of the southern Canadian Rocky Mountains.

not been placed definitely. Taylor (1957) believes that the lower part of the Flume formation is of Middle Devonian Givetian age but McLaren (*in* McLaren & Belyea 1957, and personal communication) believes that the boundary should be placed lower at the base of the Flume formation.

Stromatoporoids are most abundant in the Cairn formation but a few were collected from the Southesk formation. Most of these latter came from the Grotto member. The middle part of the Mount Hawk limestones contains stromatoporoids near its transition into the reefal Peechee member. Stromatoporoids are common in some sections of the Flume formation. Reefal lenses with stromatoporoids are rare in the Alexo formation. A stromatoporoid was collected at a single locality within the Costigan member but a specimen found loose at another locality is believed to have come from this member. The aberrant stromatoporoid *Amphipora* occurs in all the carbonate formations below the Palliser limestone. This twig-like fossil commonly occurs in such abundance that it makes up nearly half of beds several feet thick.

SYSTEMATIC PALEONTOLOGY

In the following descriptions the terminology of Galloway is used and readers are referred to his glossary (1957) for explanation of terms. The position of the numbered localities is described in the appendix and illustrated in figure 1.

Family LABECHIIDAE

LABECHIA PALLISERI, n. sp.

Pl. 105, figs. 1,2

Only two specimens of this species were collected and both encrust foreign bodies or other stromatoporoids. The largest is 10 mm. thick. One shows latilaminae about 3 or 4 mm. thick separated by lines where pigment has been deposited. Exterior surface is not preserved, but from the evidence of the sections and descriptions of similar species it must have been roughened by the emergence of the pillars as nodules, and must have risen gently into low mamelons. No trace of astrorhizae was seen.

In vertical section the thick pillars are the most conspicuous elements of the structure. The laminae are replaced in this species by a series of dissepiments or cyst-plates as is typical of the genus. They are thin, compact, well defined and of low curvature so that locally they appear to merge into continuous thin laminae. The range in size of these dissepiments is great, from 0.2 mm. in height and 0.8 mm. in length to 0.4 mm. in height and 1 mm. in length. Where the pillars are large and widely spaced the dissepiments are larger also.

The pillars are much thicker than the dissepiments and show a range of thickness even within the same section. The largest are about 0.4 mm. in diameter and much lighter in the axial zone suggesting that they are hollow; the smaller are about 0.13 mm. in diameter and do not have the lighter axial zone. Only rarely are the pillars longer than 2 mm. but their length in any section is largely determined by the orientation of the section and the sinuosity of the pillars. Where closely spaced the small pillars are about 0.3 mm. apart. The larger pillars are grouped together and seem to radiate outwards from the regions where the dissepiments are gently inflected into low mamelons.

In tangential sections the pillars appear as fine round dots, regularly spaced and about 0.1 mm. in diameter.

Discussion.—Most of the described Devonian species of *Labechia*, a typically Ordovician stromatoporoid, come from the Soviet Union. *L. palliseri* shows some resemblance to several Soviet species but most closely to *L. devonica* Riabinin and *L. polaris* Gorski. The structure of these species is much more regular than that of the Albertan species and only a single type of pillar is present in them. The Soviet species show astrorhizal canals that were not observed in *L. palliseri*. Galloway (1957) questions the Soviet Devonian occurrences of this genus but there can be no doubt that one of the specimens of this species occurs near the top of the Upper Devonian succession in Alberta. The occurrence of *Labechia* and its relatives as the last of the stromatoporoid race at the end of the Devonian may be likened to the persistance of primitive types that is commonplace in the paleontological record.

Occurrence.—Both specimens of this species in the collection are associated with rocks of the Costigan member of the Palliser formation. The holotype which is no. 15,311 in the type collection of the Geological Survey of Canada was collected loose below cliffs of the Palliser limestone at Wapiabi Gap (locality 11). The other specimen (no. 15,312) was collected in place from the Costigan member near the Elk Lakes near the boundary between Alberta and British Columbia (locality 20).*

Family CLATHRODICTYIDAE

ANOSTYLOSTROMA VESICULOSUM, n. sp.

Pl. 105, figs. 3–5; text-fig. 3

Coenosteum plate-like to massive, hemispherical, up to 60 mm. in diameter, commonly growing with and over *Alveolites*. No specimen in the collections shows the surface but the inflection of the laminae into columns associated with the astrorhizal canals indicates that the surface was covered with mamelons spaced about 7 mm. apart. Tangential sections show that a well developed astrorhizal system was associated with the mamelons. Specimens are not conspicuously latilaminate but many vertical

* After this paper was in press, another specimen of *Labechia* was obtained through A. E. H. Pedder from the Costigan member near Sunwapta Pass, Alta. It differs from the specimens described above in that the pillars are confined to small, scattered parts of the large coenosteum and most of the specimen is composed only of overlapping cysts of various sizes. It may represent an extreme variant of *L. palliseri* or may be a new species.

sections are marked by planes where growth appears to have stopped and a brown residue accumulated before growth continued.

In vertical section laminae appear to be thin, persistent, compact, distinct. They are sharply inflected into mamelon columns in most specimens but the development of these columns ranges from very marked in some specimens to rather poor in others. Practically all intermediate stages are represented. Between the inflected parts, the laminae may be only gently undulant. The laminae appear to have a median light layer locally but no well defined, transversely porous structure was detected. Laminae are spaced so that about 6 occur in 2 mm.

Dissepiments abundant, locally regularly semicircular in section and small, in other places forming elongate cysts which produce secondary laminae between the primary ones, or, in places where they are close against the upper part of the gallery, making the primary lamina appear double. Locally the combination of these dissepiments with the primary laminae give the laminae the appearance of being longitudinally fibrous as in *Synthetostroma* but this effect can be seen in isolated parts only of vertical sections.

Pillars in vertical section appear to be thicker than the laminae (i.e., about 0.1 mm. thick), spool-shaped, expanding against the laminae above and below, but more widely above than below, not breaking up into strands, locally oblique, confined to a single interlaminar space, spaced about 5 or 6 in 2 mm. In the columns the pillars are better defined, superposed, and radiate outward from the axes of the inflections of the laminae. In some sections the pillars seem to break down into a mass of unorganized tissue in the columns.

Astrorhizal tubes seen in vertical section are concentrated in the regions of the columns. These columns are locally pierced by a central canal.

Tangential sections of the areas between the columns show the pillars emerging as regularly spaced, roughly circular dots that are rarely joined into vermiculate lines. In most sections a few of the pillars are lighter in the center and resemble ring-pillars. Astrorhizal canals about 0.3 mm in diameter and highly ramified are conspicuous in the areas of the columns. The canals of larger diameter are cut by undulant, fine tabulae.

Discussion.—The assignment of Devonian species to genera of the Clathrodictyidae is difficult. Galloway (1957) has concluded that *Clathrodictyon* itself is rare in the Devonian and that most of the species that have been assigned to this genus should be placed in *Anostylostroma*. In this genus the pillars are distinct from the laminae and tend to spread out along them. The genus apparently grades through *Stictostroma* into *Stromatoporella* in which the laminae are coarsely and transversely porous and some of the pillars are formed by the inflection of the laminae (ring-pillars). In *Anostylostroma vesiculosum* the ring-like form of some of the pillars in tangential section does not seem to be the result of the upward inflection of the laminae for no such inflection can be seen in vertical section. Rather, these pillars are of the structure of those described in *A. meshbergense* Galloway & St. Jean. The species shows considerable resemblance to *Syringostroma micropertussum* Lecompte, which Galloway & St. Jean refer to the genus *Stictostroma*. Galloway's definition of *Anostylostroma* and *Stictostroma* are so close that it is difficult to see how both genera can be justified. From *Syringostroma micropertussum* the new species differs in its more widely spaced laminae and the differences between the pillars in the columns and those between the columns. In Lecompte's species the pillars are indistinct in the columns. The new species also has a general resemblance to *Syringostroma tuberosum* Galloway & St. Jean but does not show the maculate tissue of this species or of the genus *Syringostroma* as defined by these authors. None of the species described by Galloway or Parks (1936) have the abundance of dissepiments found in *A. vesiculosum*.

Occurrence.—This stromatoporoid is one of the more common species in the Fairholme group and many specimens are well preserved. The species is common in the Cairn formation but some of the specimens in the collection come from the Southesk formation. The type specimen comes from the south side of Isaac Creek at Mount Sawtooth in Jasper National Park (locality 15) and is no. 15,313 in the Geological Survey of

Canada type collection. Localities: 4, 5, 9, 12, 13, 15, 16, 17, 21, 22.

ATELODICTYON STELLIFERUM, n. sp.
Pl. 105, figs. 6–8

Coenosteum hemispherical, regular, massive. Surface not preserved but is assumed from the evidence of sections to have risen into low, broad mamelons. Astrorhizae well developed, apparently associated with the mamelons.

In vertical sections the laminae are thin, regular, only slightly undulant, appearing in thin, well-preserved sections as a series of granules, not as solid lines, composed of projections from the pillars and, therefore, highly porous. Spacing of laminae variable ranging from 6 to 12 in 2 mm. in different parts of the same section. Laminar structure breaks down into formless fibers a few millimeters from the outside edge of the coenosteum.

Dissepiments not abundant, scattered irregularly throughout the structure. Only locally are they present in sufficient quantity to build up secondary laminae, generally they are a minor element of the structure. Galleries higher than long, rounded.

Pillars confined to a single interlaminar space, thicker than the laminae (0.07 mm.) and not as sharply defined, positioned at right angles to the laminae, spreading slightly at the top but showing no obvious tendency in vertical section to divide upwards, only rarely superposed. Many pillars appear to be incomplete and do not reach the lamina above.

In tangential section the pillars appear between the laminae to be a series of round dots about 0.1 mm. in diameter. At the laminae these are joined to their neighbors to form a network with pores about 0.1 mm in diameter. Lamina therefore appear in tangential sections as a net.

Astrorhizal canals are prominent in both tangential and vertical sections especially in the vicinity of the mamelons. Canals are up to 0.5 mm. in diameter.

Discussion.—The genus *Atelodictyon* differs from *Actinostroma* in that the pillars are not continuous through the laminae, but the laminae are formed in the same way, by radial processes given off from the pillars. It differs from *Anostylostroma*, which it superficially resembles, in the presence of the radial processes. Only a few species of this genus have been described. *Atelodictyon stelliferum* differs from the type species *A. fallax* Lecompte in the much greater irregularity of its structure. It is similar to *A. intercalare* Galloway & St. Jean but has low mamelons, less distinct pillars, more continuous laminae, and more prominent astrorhizal canals. From *A. ordinata* described below this new species differs in the much greater simplicity of its pillar structure.

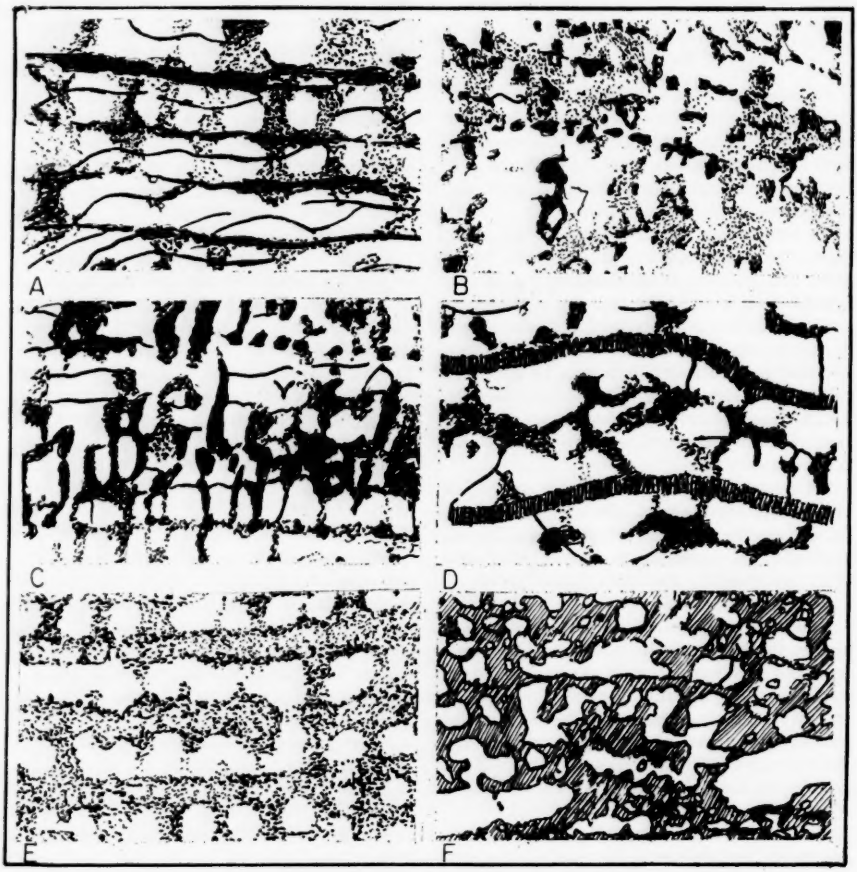
Occurrence.—This species is not common in the Fairholme group. At two localities where the fossil was collected in place, the species occurs in the Cairn formation; at the third in the base of the Flume formation. The type specimen comes from the Cairn formation at the southern end of the Ram Range, Alta. (locality 6) and is no. 15.315 in the Geological Survey of Canada type collection. Localities: 1A, 6, 17, 22.

ATELODICTYON ORDINATUM, n. sp.
Pl. 105, fig. 9; Pl. 106, fig. 1; text-fig. 3

The species is based on a single coenosteum which is about 10 cm. in diameter, cabbage-shaped, subspherical. Its surface is not well preserved but apparently it was smooth and without mamelons. No astrorhizae were observed on the surface but sections indicate their presence at some levels in the coenosteum.

Vertical sections show well defined, persistent laminae and pillars. The laminae are regularly curved and not bent upward into mamelons. They are not continuous but are made up in section of compact granules. The spaces between the granules represent pores in the laminae by which the galleries are confluent. The laminae are widely spaced about 1 mm. apart.

Pillars are confined to a single interlaminar space. They are about 0.08 mm. thick, composed of granular tissue with some pores which, however, does not appear to be maculate. They arise from the laminae, may bifurcate and join irregularly with adjacent pillars to form a somewhat irregular vertical structure, but fall short of the overlying laminae generally by about 0.2 mm. This conspicuous clear space in the structure is crossed by a few pillars and by a few large dissepiments. Smaller dissepiments are ir-



TEXT-FIG. 3—Sketches of vertical sections of stromatoporoids magnified 30 times. The dotted pattern indicates only the density of the tissue as seen in sections and does not reflect a maculate structure. The sketches were made on enlarged photographs except B which was drawn by projection.

A. *Anostylostroma vesiculosum*, n. sp., showing poorly defined spool-shaped pillars and abundant dissepiments.

B. *Atelodictyon stelliferum*, n. sp., showing three laminae in the upper part of the sketch composed of discrete dots and the highly irregular pillar structure.

C. *Atelodictyon ordinatum*, n. sp., showing two laminae separated by complex branching pillars.

D. *Hammatostroma albertense*, n. gen., n. sp., showing the transversely porous laminae and tangled pillars.

E. *Taleastroma lenzi* Galloway, showing the imperfect superposition of the pillars and thick laminae with a median light zone.

F. *Ferestromatopora jacquensis* Galloway, showing the irregular structure with tissue cross-hatched.

regularly and sparsely scattered in the structure. Although the pillars are in general perpendicular to the laminae, many of the individuals are oblique.

In tangential section the pillars emerge as round dots that appear to be somewhat porous. Between the laminae these pillars are isolated, but where the plane of the lamina has been cut they are joined by radial processes to their neighbors to form a network. The clear area beneath the laminae can be distinguished in tangential section as a band occupied by a few pillars. In tangential sections astrorhizal canals ramified, about 0.5 mm. in diameter, and crossed by thin tabulae are common.

Discussion.—This species is characterized by the complexity of the pillars, the wide spacing of the laminae, and the clear zone associated with each lamina. The ramifying pillars confined to a single interlaminar space but joined to produce a highly porous lamina place this species in the genus *Atelodictyon*. *A ordinata* differs from the type species *A. fallax* Lecompte in the much coarser texture of its structure, and the greater ramification of its pillars. In this latter feature it resembles *A. intercalare* Galloway & St. Jean but has a much more regular laminar structure than this species. The apparent porosity of the pillars may be a result of the type of preservation but if not it suggests that the species may be related to *Trupetostroma*. However, the nature of the laminae preclude this assignment.

Occurrence.—The single specimen was collected from a bed 519 feet above the base of the Cairn formation in the Ram Range, Alta. at locality 6 and is no. 15,317 in the Geological Survey of Canada type collection.

HAMMATOSTROMA, n. gen.

Stromatoporoids related to *Stromatoporella* and *Anostylostroma* in which the laminae are persistent, undulant, transversely porous, and in which the interlaminar spaces are occupied by an irregular tangle of transversely porous pillar tissue arising from the laminae, and by dissepiments. The pillars pass from one lamina by highly irregular and in part oblique and horizontal courses to the lamina above and are cut in vertical section only for short segments so that they appear as dots or short horizontal or oblique lines. Astrorhizae absent to abundant. Type species: *Hammatostroma albertense*.

Discussion.—The group of species that are here united to form a new genus appear to be a branch of stromatoporoids related to *Anostylostroma* and *Stromatoporella*. Unlike the former the pillars do not form rings in tangential section and do not appear to be formed by the bending of the laminae. Unlike the latter the pillars rarely cross an interlaminar space directly. The genus can therefore be placed in the family Clathrodictyidae of Galloway. Only the type species of *Hammatostroma* occurs in the Devonian of Alberta but a study of the literature reveals that several other species have been described that have the structure of the genus and Dr. J. J. Galloway (personal communication) has kindly pointed out other species that might be placed in it. These species have been described as belonging to *Clathrodictyon*, *Stictostroma*, and *Stromatoporella*.

The earliest state in which the tangled structure of *Hammatostroma* can be recognized is found in *Clathrodictyon carnicum* Charlesworth from the Lower Devonian of the Alps. In this species the pillars are largely thorn-like projections from the laminae but locally they give rise to a highly irregular structure within the interlaminar space and produce impersistent secondary laminae between the primary ones. The tendency for tangling is further advanced in *Clathrodictyon katavensis* Yavorsky, which Riabinin (1932) regards as very similar to *Clathrodictyon tschussovensis* Yavorsky and *Clathrodictyon carnicum* Charlesworth. He believes that characters of all three species can be found in a single section. In *Stictostroma jeffersonvillense* Galloway & St. Jean (which Dr. Galloway has suggested belongs in this group) some of the pillars still cross the interlaminar space but most of them turn obliquely to form impersistent secondary laminae between the primary ones. *Stromatoporella undata* Yavorsky also shows some pillars or irregular shape crossing the space directly but most form between the laminae the structure typical of *Hammatostroma*. Many dissepiments are present in the interlaminar space of this species. *Stromatoporella insolita* Yavorsky shows the

transition of the *Hammatostroma* structure to *Stromatoporella*. Although in vertical section the pillars follow an irregular, tortuous course, tangential sections show so many well developed ring-pillars that this species is probably best retained under the genus *Stromatoporella*. In *Hammatostroma albertense* the tangled pillar structure is such that no pillars pass directly from lamina to lamina but all are caught up in the irregular tangle that may produce locally one or more secondary laminae between the primary ones.

In summary, the following species can be placed in the new genus:

Hammatostroma carnicum (Charlesworth)
H. tschussovensis (Yavorsky)
H. katavensis (Yavorsky)
H. undata (Yavorsky)
H. jeffersonvillense (Galloway & St. Jean)
H. albertense Stearn

HAMMATOSTROMA ALBERTENSE, n. sp.
Pl. 106, figs. 2,4; text-fig. 3

Coenosteum represented by fragments only in the collection, apparently spheroidal, massive, commonly associated with other stromatoporoids. Surface observed only in section; rising into low mamelons a few millimeters high. Astrorhizae not observed in tangential sections and may be absent.

In vertical section the structure is very regular with few breaks of growth or inclusions of foreign material. The laminae are the most prominent structures. They are gently undulant, in places rising into low mamelons but not sharply inflected into mamelon columns, less than 0.1 mm thick, clearly transversely porous, spaced widely so that they are about 1 mm. apart and 3 occur in 2 mm.

Pillars arise from the laminae as short, thorn-like projections but in no place are continuous across the interlaminar space. Apparently they turn in the central part of the space and entwine irregularly in a direction subparallel to the laminae. The subparallel sections of their structures form secondary laminae but only for short distances and much of the pillar structure appears as small dots in vertical section. The complexity of the tangling varies somewhat from section to section and to a certain extent within the same section. Its complexity can best be appreciated through reference to the illustrations. Dissepiments are common in vertical sections.

In tangential section the laminae appear as well defined dark lines without foramina. The pillar structure appears as a series of dots which are commonly and irregularly joined to their neighbors. In places vague ring structures may appear but no well defined ring pillars were observed. Locally

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EXPLANATION OF PLATE 105

All figures magnified 10 times.

FIGS. *1,2*—*Labechia palliseri*, n.sp. *1*, vertical section of holotype (G.S.C. 15,311) showing two sizes of pillars penetrating a structure of cysts of low curvature; *2*, tangential section of same specimen. Locality 11.

3–5—*Anostylostroma vesiculosum*, n. sp. *3*, tangential section of holotype (G.S.C. 15,313); *4*, vertical section of holotype showing a mamelon column pierced by an axial canal. Locality 15. *5*, vertical section of another specimen (G.S.C. 15,314) in which the columns are poorly developed. Locality 12.

6–8—*Atelodictyon stelliferum*, n. sp. *6*, vertical section of holotype (G.S.C. 15,315) showing irregular pillars, granular laminae and abundant astrorhizal canals. Locality 6. *7*, vertical section of another specimen (G.S.C. 15,316) in which the laminae are more regular. Locality 22. *8*, tangential section of holotype showing the abundant astrorhizae and the porous nature of the laminae.

9—*Atelodictyon ordinatum*, n. sp. Tangential section of the holotype (G.S.C. 15,317) showing the nature of the pillars and the porous laminae. Locality 17.

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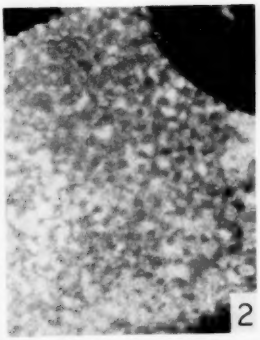
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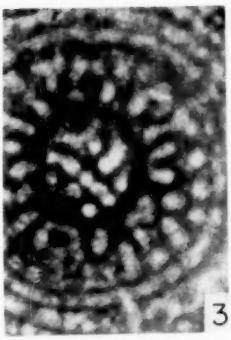
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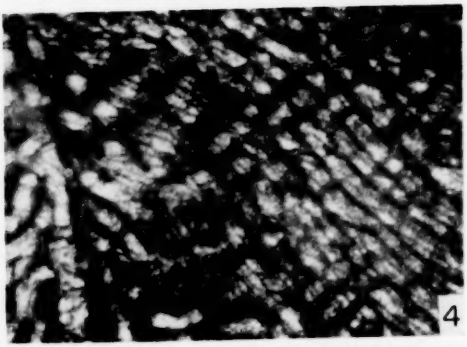
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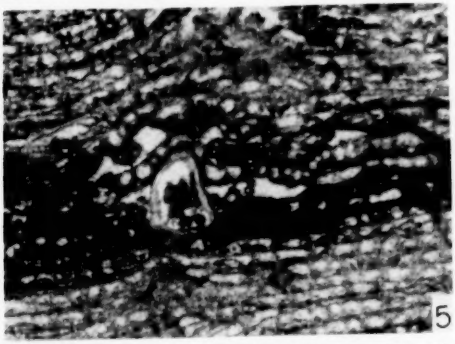
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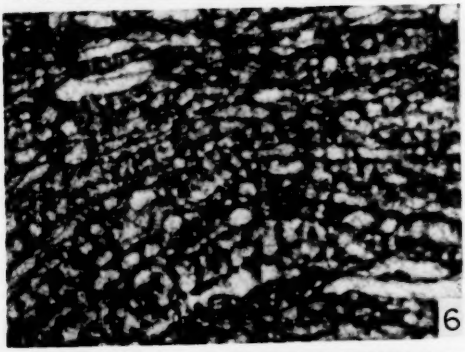
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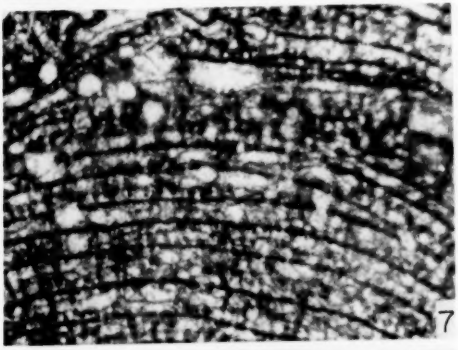
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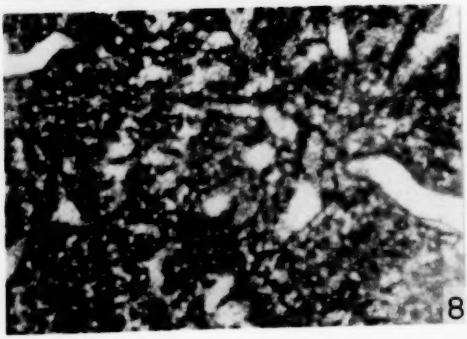
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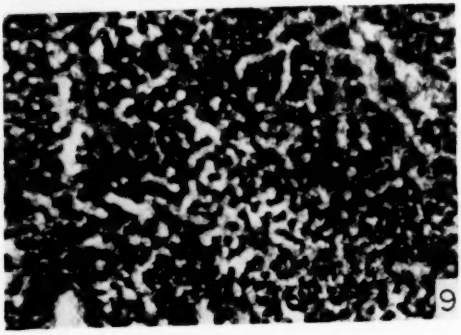
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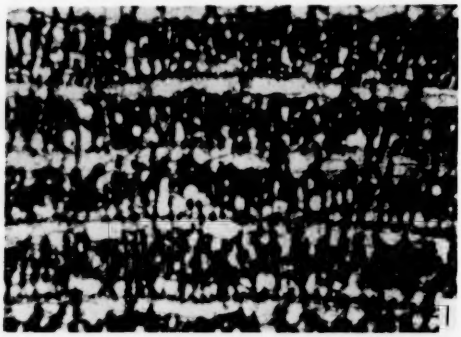
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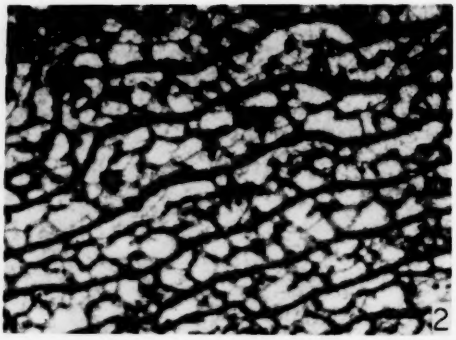
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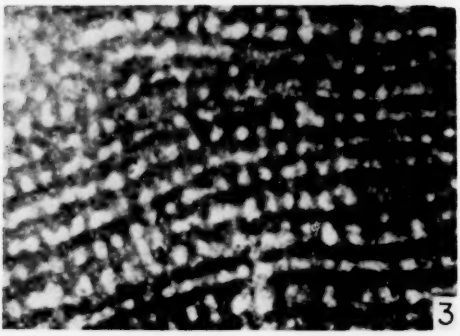
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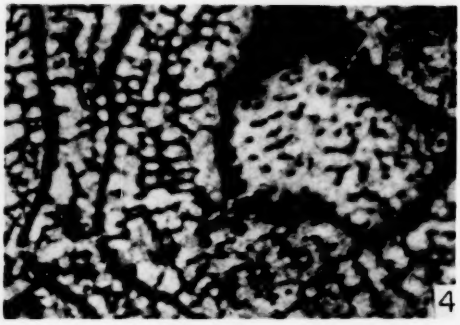
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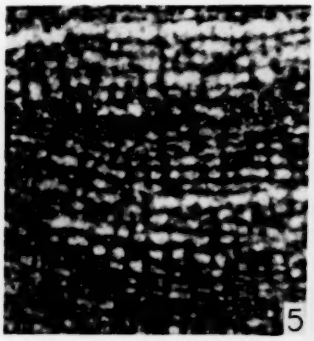
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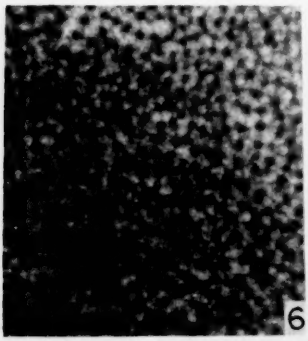
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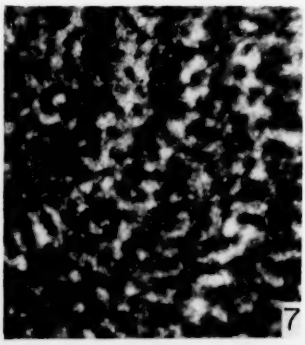
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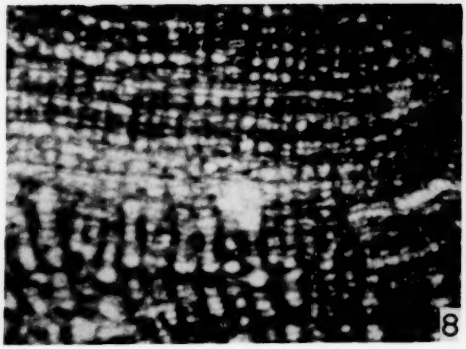
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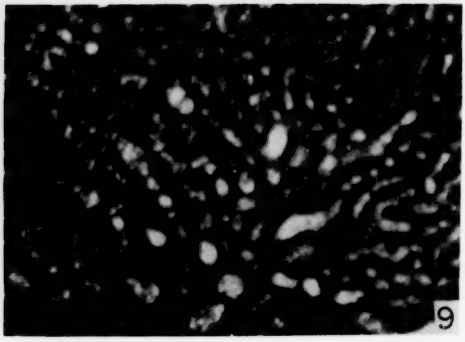
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fine canals seem to run through the structure but these are not typical astorhizae.

Discussion.—*Hammatostroma albertense* is characterized by the intensity of the tangling of the pillars so that none of them crosses the interlaminar space directly. Its structure has been compared with that of other species assigned to the genus above.

Occurrence.—The species has been found in four widely separated localities in the Devonian of Alberta. The type specimen comes from the Cairn formation at the south side of Isaac Creek at Mount Sawtooth (locality 15) and is no. 15,318 in the Geological Survey of Canda type collection. Other specimens come from the Cairn and Southesk formations. Localities: 9, 13, 15, 17.

Family ACTINOSTROMATIDAE
ACTINOSTROMA DEVONENSE Lecompte
Pl. 106, figs. 5, 6

Actinostroma devonense Lecompte, 1951, p. 88–90, pl. II, figs. 3–6; pl. III, figs. 1–3.

Coenosteum generally small, up to 60 mm. in diameter, massive, hemispherical. Surface not exposed but apparently smooth and without mamelons. Growth in some specimens appears to be latilaminate with zones about 4 mm. thick.

In vertical section the laminae appear to be continuous and can be traced for many millimeters. With the pillars they form a regular network in which neither element of the structure is consistently more prominent. Laminae are generally slightly undulating, generally closely parallel, and only slightly and locally crinkled, thin, less than 0.1 mm. in thickness, apparently compact, spaced so that about 12 to 14 occupy 2 mm.

The pillars in vertical section are locally less well defined than the laminae and thicker (0.2 mm.). They appear to be hazy in some states of preservation. In accurately oriented sections they pass through 8 to 10 laminae. Pillars are spaced about 6 to 8 in 2 mm. or slightly farther apart than the laminae. Galleries are equidimensional to wider than high, rectangular, with rounded corners. Dissepiments are rare and do not appear to be part of the normal structure. Pillar tissue is compact.

In tangential section the pillars emerge as round dots about 0.2 mm. in diameter. In the laminae these dots are connected to their neighbors by processes to produce a network. The laminae appear to be pierced by large circular foramina. The astrorhizal system is poorly defined but can be detected in the alignment of pillars in tangential sections.

The species is characterized by the regular network of pillars and laminae and the spacing of these elements of the structure.

EXPLANATION OF PLATE 106

All figures magnified 10 times.

FIG. *1*—*Atelodictyon ordinatum*, n. sp. Vertical section of holotype (G.S.C. 15,317) showing pillar structures. Locality 17.

2,4—*Hammatostroma albertense*, n. gen., n. sp. *2*, vertical section of holotype (G.S.C. 15,318) showing continuous laminae and irregular pillars. Locality 15. *4*, tangential section of holotype.

3,7—*Taleastroma lenzi* Galloway. *3*, vertical section (G.S.C. 15,320) showing superposed pillars and prous laminae; *7*, tangential section. Locality 13.

5,6—*Actinostroma devonense* Lecompte. *5*, vertical section (G.S.C. 15,319). Locality 1. *6*, tangential section of same specimen showing radial processes emerging from pillars.

8–9—*Trupetostroma lecomptei*, n. sp. *8*, vertical section of holotype (G.S.C. 15,321) between two columns showing the persistent pillars and laminae. Locality 22. *9*, tangential section across side of a column of the holotype.

Discussion.—Many Devonian stromatoporoids have been described with the regular network of *Actinostroma clathratum* Nicholson. They include such species as *A. compacta* Ripper, *A. timanicum* Riabinin, *A. salaricum* Yavorsky, *A. egregium* Yavorsky and *A. devonense* Lecompte. These species differ largely in the regularity of their structure and the spacing of the skeletal elements. The preservation of the radial processes that connect the pillars in tangential section (hexactinellid network) is variable in the Albertan specimens and seems to be the first structure to be obscured in dolomitization. Ripper (1938) has divided *Actinostroma* into several groups on the basis of this character but her division is criticized by Lecompte (1951) who points out that the nature of the network formed by the radial processes may vary within the same species or specimen.

Actinostroma devonense differs from *A. clathratum* largely in the spacing of the pillars. The specimens from Alberta do not show the great regularity of structure nor the beauty of the hexactinellid network of the Belgian specimens but seem to be conspecific. *A. devonense* Lecompte has more closely spaced laminae than *A. compacta* Ripper and shows a tendency for the galleries to be wider than high.

Occurrence.—This stromatoporoid is one of the commonest in the Devonian of Alberta. Stratigraphically it has been found in both the Cairn and Southesk formations of the Fairholme group, and in the Alexo formation. Localities: 1, 3, 3A, 8A, 10, 14, 17, 21, 22, 22A, 25B.

TRUPETOSTROMA LECOMPTEI, n. sp.
Pl. 106, figs. 8, 9

Coenosteum subspherical, free, about 7 cm. in diameter in the specimens at hand, showing no sign of latilaminate growth externally. Surface not preserved on any specimens but from the evidence of the vertical sections it must have risen regularly into well defined mamelons from which astrorhizal canals radiated.

Vertical sections show well defined pillars and laminae, both apparently continuous and compact. As in most species of this genus the pillars are thicker than the laminae and are the more conspicuous element of the structure. Laminae are in most places very fine and compact, gently undulant but locally inflected into mamelon columns that are about 10 mm. apart. They show a poorly defined, crinkled appearance in some regions. Locally they are thickened by less dense tissue, perhaps in zones where the rate of growth was irregular. Spaced about 15 in 2 mm. and locally grouped where two or three laminae are closer together than their neighbours. Dissepiments uncommon.

Pillars thicker than laminae (0.2 mm.) lighter in color, not as dense but with no obvious vacuoles, regularly superposed from lamina to lamina so that they appear to pass through 7 or 8 of them, somewhat, but not conspicuously, thickened at the laminae. Galleries almost circular in vertical section. Astrorhizal canals conspicuous in vertical sections especially near the mamelon columns. Pillars spaced about 6 or 7 in 2 mm.

In tangential section the radial and concentric structure of the mamelon columns is conspicuous. Between them the pillars emerge as round, discrete dots, generally unconnected to their neighbours. The laminae appear to be minutely porous in tangential section. In the columns the pillars and laminae combine to form a regular hexagonal network. Astrorhizal canals 0.5 mm. across radiate from these columns but a central axial canal does not seem to be present.

Discussion.—*Trupetostroma lecomptei* is similar to *T. tenuilamellatum* Lecompte. The nature and spacing of the pillars and laminae are practically identical and the two species differ only in the conspicuous inflection of the laminae of *T. lecomptei* into columns. This inflection is poorly developed in the Belgian species and Lecompte states that no mamelons were observed on the surface. Until characters that constitute varietal differences in the stromatoporoids are decided, this group of specimens is named as a new species.

Occurrence.—This stromatoporoid is common in the basal part of the Fairholme group. Of the five localities from which this species was definitely identified, three are in the lower part of the Cairn formation and two are in the Flume formation. The type

specimen comes from locality 22 and is no. 15,321 in the type collection of the Geological Survey of Canda. Localities: 18, 19, 22, 24, 25.

TRUPETOSTROMA TENUE, n. sp.
Pl. 107, figs. 1–3

Coenosteum subspherical, massive, in one specimen 8 cm. in diameter. Surface smooth and regular, apparently without astrorhizae as indicated by tangential sections. Growth is not latilaminar.

In vertical section the pillars and laminae form a regular network in which each element is of equal importance. The laminae are thin (about 0.1 mm.) gently curved along the contour of the coenosteum, composed apparently of a thin dark line on which is imposed lighter secondary material spreading from the pillars. Spaced about 8 in 2 mm.

Pillars in general Y-shaped, spreading markedly at the base of the lamina above and locally porous at the top, spreading slightly at the base but not as conspicuously as at the top. About three-quarters are regularly superposed from lamina to lamina to form a structure similar to that of *Actinostroma*. A few of the pillars are incomplete. Pillars are spaced about 8 to 10 in 2 mm. and are about 0.1 mm. thick. Galleries are regularly superposed, equidimensional with rounded corners. Dissepiments are absent. Foramina piercing the laminae are rare. The pillar tissue is compact but the vacuolate nature of the pillars typical of the genus *Trupetostroma* is not well developed in this species.

In tangential section the laminae are well defined as darker lines pierced by a few small pores. Between the laminae the pillars emerge as subrounded dots about 0.1 mm. across. No evidence of an astrorhizal system was noted.

Discussion.—This species shows a structure reminiscent of *Actinostroma* but is distinguished from it by the upward spreading, partly vacuolate pillars which locally contribute tissue to the thin laminae. It is distinguished from *T. lecomptei*, n. sp., by the greater spacing of the laminae, the lack of mamelon columns, and the form of the pillars. The structure is similar to that of *T. warreni* Parks but the pillars are relatively thinner and the laminae thicker. In general, all the species of *Trupetostroma* described by Lecompte (1952) have much thicker pillars than *T. tenue*.

Occurrence.—This species is represented by a single, very well preserved coenosteum from 180 to 200 feet above the base of the Cairn formation, two miles southeast of Obstruction Mountain. This specimen is the type and is no. 15,322 in the Geological Survey of Canda collections. Locality: 7.

Family STROMATOPORIDAE
FERESTROMATOPORA JACQUENSIS Galloway
Pl. 107, figs. 4–5; text-fig. 3

Ferestromatopora jacquensis Galloway, 1960, p. 627, pl. 74, figs. 1a,b.

Coenosteum hemispherical to subspherical, massive, up to 9 cm. in diameter in the specimens of the collection. Surface not preserved but apparently smooth and without mamelons from the evidence of the sections. Latilaminar growth not conspicuous.

Vertical sections show the laminae are dominant over the vertical pillars but the structure as a whole is irregular and in many places breaks down into tissue in which neither pillars nor laminae are distinguishable. The regular structure forms about two thirds of vertical sections. Laminae are thick (0.1 mm.) persistent in parts of the sections where regular structure is present, gently undulant, not deflected into columns, spaced about 7 to 8 in 2 mm. but only rarely can the laminar structure be traced through a height of 2 mm.

Pillars are about the same thickness as the laminae. They are highly irregular, tortuous, branching, rarely traceable as entities through more than a single interlaminar space, commonly, more or less perpendicular to the laminae. Pillars spaced about 7 or 8 in 2 mm. but spacing is irregular. Galleries in the regular parts of the structure are equidimensional and almost square in section but in many parts they are highly irregular in shape and difficult to distinguish from the astrorhizal canals which penetrate vertical sections in great numbers. Dissepiments rare, scattered irregularly in the structure. Pseudozooidal tubes missing. Vertical sections cut many astrorhizal canals

at various angles. They are about 0.8 mm. in diameter and crossed by thin, undulant tabulae.

Tangential sections are about half occupied by tissue. Laminae can be distinguished as dark lines crossing the sections. Pillars coalesce to form irregular vermicular lines which appear to be porous. A few dissepiments join these pillars. Astrorhizal canals are prominent in tangential sections. They are long, straight, with sharply defined borders, slightly less than 1 mm. in diameter.

Tissue is finely maculate in both tangential and vertical sections.

Discussion.—The specimens from Alberta agree well with Galloway's description of the species from the *Radiastraea arachne* zone, north of Norman Wells. The Alberta specimens do not appear to be as coarsely maculate as the specimen figured by Galloway and they seem to have more astrorhizal tubes which are prominent in both vertical and tangential sections.

Occurrence.—Specimens of this species come from the collections supplied by A. E. H. Pedder and were collected from the Cairn and Flume formations. Localities: 22, 22A.

STROMATOPORA cf. COOPERI Lecompte
Pl. 107, fig. 6

Stromatopora cooperi Lecompte, 1952, p. 285–288, pl. LIX, fig. 2; pl. LX, figs. 1–4.

Coenosteum generally hemispherical but encrusting in some specimens, commonly associated with the coenostea of other stromatoporoids. Surface not preserved but the evidence of the sections indicates that it was smooth, without mamelons but marked by prominent astrorhizae.

In vertical sections the large sub-parallel pillars are the most conspicuous feature and no true laminae exist. The pillars are closely set so that about 8 occupy the space of 2 mm. They are about 0.15 to 0.20 mm. in diameter. They are separated by thin convex dissepiments which divide high narrow galleries, the zooidal tubes of Nicholson and the pseudozooidal tubes of Galloway. The dissepiments are irregularly spaced about 6 to 10 in 2 mm. The pillars branch and unite irregularly and locally the structure breaks down into a network in which vertical and horizontal elements cannot be distinguished. Growth is latilaminar but the zones which are marked by more highly pigmented layers are only 3 to 4 mm. thick. In vertical section round or elongate astrorhizal canals are common, particularly at certain levels and in certain sections. These are about 1 mm. in diameter and crossed by thin, plane tabulae. The tissue appears to be finely maculate but is not in a good state of preservation.

In tangential section the pillars form an irregular network of maculate tissue. Astrorhizal canals crossed by fine tabulae are prominent and about 1 mm. in diameter but branching to smaller sizes.

Discussion.—The Canadian specimens show considerable resemblance to *Stromatopora planulata* (Hall and Whitfield). The resemblance of this species to *Stromatopora cooperi* Lecompte has been discussed at length by Lecompte (1952). The specimens described here differ from the *Stromatopora planulata* ? of Galloway (1960) in not showing the dark ring of tissue around the galleries, in the greater prominence of the pillars, and in the suppression of the horizontal elements. The uncertainty concerning the types and identity of *Stromatopora planulata* would suggest that the name is best avoided. The specimens from Alberta are provisionally referred to *S. cooperi* because of their close resemblance to this species in gross structure. The vertical development of the pillars is not as strong in the Albertan specimens as in those from Belgium and the latilaminae are not as thick, but these differences do not appear to be of specific value in the light of their variability in the forms described by Lecompte.

Occurrence.—This species is not uncommon at the top of the Cairn formation of the Fairholme group. Localities: 1A, 2, 9, 14.

TALEASTROMA LENZI Galloway
Pl. 106, figs. 3, 7; text-fig. 3

Taleastroma lenzi Galloway, 1960, p. 630, pl. 75, figs. 2a,b.

Coenosteum massive, hemispherical or encrusting. The largest specimen in the collection is 40 mm. in diameter. One of the specimens encrusts a calcareous cylinder that may be a nautiloid, another is associated with *Labechia palliseri*. No surface

characteristics were obsreved but the laminae do not rise into mamelons and therefore the surface was probably smooth. Astrorhizal canals were not observed in these specimens and are possibly absent in the species.

In vertical section the laminae and pillars form a regular network, each element of about equal prominence. The laminae are thick (0.3 mm.), gently undulant, highly persistent, consisting of a central highly porous zone and lateral denser tissue. Some sections show this central zone to be transversely porous but in most places this structure cannot be seen and the laminae merely appear to be double. Locally the laminae are interrupted by the passage of a large pore or foramen. Laminae spaced about 4 to 6 in 2 mm. The galleries in vertical section are rounded and roughly equidimensional. Dissepiments are absent.

Pillars in vertical section generally thinner than laminae, spool-shaped, thickenned more markedly above than below, locally incomplete. Pillars appear to pass through laminae but locally this "superposition" is not marked. They are locally darker and granular on the exterior and lighter on the interior. They are spaced about 6 in 2 mm.

In tangential section the laminae appear to be discrete plates pierced by large foramina. Between the laminae the pillars emerge as round dots not joined to their neighbours but near the laminae they become joined. No astrorhizal canals appear in tangential sections.

Discussion.—Unfortunately the fine structure of this species has been poorly preserved and the identification of the genus *Taleastroma* depends on the preservation of the maculate borders of the pillars. Locally this structure is suggested by the hollow appearance of the pillars but generally it is not preserved. However, the dimensions and gross structure of the stromatoporoid are so close to that of *Taleastroma lenzi* described by Galloway from the *Radiastraea arachne* zone of the Ramparts formation that it is identified as such.

Occurrence.—Specimens of this species have been collected from the Cairn, Southesk, Alexo, and Palliser formations. Localities: 11, 13, 14, 23, 24.

CLATHROCOILONA cf. SPISSA (Lecompte)
Pl. 107, figs. 7,8

Stromatoporella spissa Lecompte, 1951, p. 187–189, pl. XXVII, figs. 1–4.

Coenosteum massive, latilaminar, hemispherical, probably also encrusting, in some specimens growing over and around colonies of *Alveolites*. Surface probably irregular and rising into low mamelons as indicated in vertical sections but not observed directly.

In vertical section laminae are gently undulant, locally well defined, locally merging into structureless pigmented tissue, showing a well defined central porous zone or apparently longitudinally fibrous. Where a series of laminae can be distinguished about 10 occupy 2 mm. A considerable part of the structure consists of irregular tissue of granular aspect In which neither pillars nor laminae can be distinguished. Vertical sections commonly show inclusions of other fossils or lenses of sediment and irregular levels of more intense pigmentation along which growth appears to have ceased for a time and then been resumed. Pillars can be recognized only locally as short, spool-shaped, and confined to a single interlaminar space. Galleries in vertical section are rounded, circular to irregular, crossed by scattered dissepiments.

Astrorhizal canals about 0.4 mm. in diameter are commonly cut by vertical sections and appear as round holes or tabulate tubes. They are concentrated where the laminae turn up in the axis of a mamelon.

Tangential sections show only the astrorhizal canals embedded in tissue with vague, vein-like markings.

Discussion.—*Stromatoporella spissa* is described by Lecompte as similar to *Stromatopora rugosa* Lemaitre and in part both stromatoporoids seem to show the structure of *Stromatopora*. However, the relationship of this species to *Stromatoporella* is shown by the central porous region of the laminae. The specimens from the Fairholme group belong to the series of stromatoporoids described by Lecompte as *Stromatoporella spissa*, *S. obliterata*, and *S. irregularis* but are not identical with any of these. None of these species is typical of the genus *Stromatoporella* but they are similar to

species described by Yavorsky (1931) and Galloway & St. Jean (1957). Galloway places the first of Lecompte's three species in *Stromatopora* ?, the second in *Stictostroma*, and the third in *Clathrocoliona*. The laminae with the porous central zone, the unsuperposed spool-shaped pillars, and the granular aspect of the tissue suggest that the specimens from Alberta belong to the genus *Clathrocoliona*. Because their gross structure is similar to that of *Stromatoporella spissa* they are provisionally assigned to this species until more material is available. The structure is similar to that of *Clathrocoilona abeona* that is illustrated by Galloway (1960) from the Kee Scarp reef of the Northwest Territories. However, the Albertan specimens appear to be so different from these of *C. abeona* illustrated by Galloway and St. Jean (1957) from the Logansport limestone, and from the type specimens figured by Yavorsky (1931) and Galloway (1957) that they are provisionally referred to Lecompte's species.

Occurrence.—The specimens described here were found at two localities both within the Southesk formation. The species is abundant in a thin bed of argillaceous limestone within the reefal dolomites of the Southesk formation at Saracenhead Mountain (locality 12). Localities: 9, 12.

Family IDIOSTROMATIDAE
AMPHIPORA RAMOSA (Phillips)
Pl. 107, figs. 9, 10

Caunopora ramosa Phillips, 1841, Figures and descriptions of the Paleozoic fossils of Cornwall, Devon, and West Somerset, p. 19, pl. 8, figs. 22*a–c*.

Coenostea stem-like about 1.5 to 2.5 mm. in diameter for average specimens but specimens up to 4 mm. in diameter are not rare. Composed of a zone of amalgamated structure in which pillars and laminae cannot be distinguished surrounding an axial canal.

In cross section the canal ranges in diameter from 0.6 mm. to 1.0 mm. and is enclosed by a wall of transversely fibrous structure pierced locally by pores. The axial canal is missing from some specimens. Outside the axial zone the structure is irregular but consists of an network of pillars and laminae about 0.1 mm. thick which have a median dark line and transverse fibers radiating from it. The structural elements occupy about half of the space in this zone, the rest is open. A peripheral zone of large vesicles bounded by a wall that is also fibrous and pierced by pores is usually but not universally present.

In axial section the axial canal is prominent and crossed by fine, irregular tabulae. Its wall is pierced by pores which lead into the zone of irregular structure in which neither pillars nor laminae can be distinguished. The outer zone of large vesicles is also crossed by fine tabulae subparallel to the axis of the coenosteum.

Discussion.—The great variability of this species has recently been discussed at length by Lecompte (1952, p. 325–329) and Galloway & St. Jean (1957, p. 233–236). Within a single section such variability is found that the recognition of different species in the large number of specimens available is difficult. Some specimens have the wide axial canal, small diameter, and lack of marginal vesicles characteristic of *Amphipora laxeperforata* Lecompte but they also have tabulae in the axial canal, a feature not found in this species. Other variants are similar to *A. pinguis* Yavorsky. Until a detailed study of the variability of this aberrant stromatoporoid in the Devonian of Alberta is undertaken, the specimens in the collection are referred to Phillips' typical species.

Occurrence.—This species occurs in great abundance in the Fairholme group particularly at its base where it is an important rock-forming organism. The species has been found as high in the succession as the Alexo formation in rocks that are of Upper Devonian age.

APPENDIX

List of numbered localities:

1. Where the Ram River flows through the Second Range of the Rockies (sec. 8, tp. 35, ra. 15 W. 5th mer.). Cairn formation.
   1A. Loose at this locality.
2. Whiterabbit Range at its intersection with Twin Falls Creek (sec. 3, tp. 35, ra. 16 W. 5th mer.). Cairn formation.
3. Near headwaters of Hummingbird Creek at Second Range (sec. 26, tp. 35, ra. 16, W. 5th mer.). Southesk formation, 710 ft. above base of the Fairholme group.

3A. Lower 500 feet of Cairn formation at this locality.

4. Near crest of Ram Range, about 1 mile north of Ram River (sec. 17, tp. 36, ra. 14 W. 5th mer.). Cairn formation.
5. Headwaters of North Fork of Hummingbird Creek at Second Range (sec. 4, tp. 36, ra. 16 W 5th mer.). Cairn formation.
6. Ram Range at the second major creek tributary to Hummingbird Creek (sec. 19, tp. 36, ra. 14 W. 5th mer.). Cairn formation.
7. Two miles southeast of Obstruction Mountain, Fourth Range (lat. 52°22′ N., long. 116°52′ W.). 180–200 ft. above base of Cairn formation.
8. Ram Range on north side of Cripple Pass (sec. 8, tp. 37, ra. 15, W. 5th mer.). Middle Mount Hawk limestone.

   8A. Flume formation at same locality.
9. Bighorn Range at the gap of Blackstone River (sec. 22 tp. 42, ra. 18 W. 5th mer.). Southesk formation, Grotto member.

   9A. Top of Cairn formation at this locality.
10. Bighorn Range midway between the gaps of Wapiabi and Blackstone Rivers (sec. 36, tp. 41, ra. 18 W. 5th mer.). Cairn formation, 95 ft. above base of exposure.
11. Bighorn Range at Wapiabi gap (sec. 21, tp. 41, ra. 17 W. 5th mer.). Loose below cliff of Palliser limestone.
12. Saracenhead Mountain south of intersection of Southesk and Cairn Rivers (sec. 35, tp. 42, ra. 21 W. 5th mer.). Argillaceous interbed in the reefal dolomite.
13. Three miles west of Cairn Pass near the headwaters of the Medicine Tent River (sec. 25, tp. 43, ra. 23 W. 5th mer.). Alexo formation.
14. Headwaters of the east branch of the first tributary of Job Creek from the east (sec. 16, tp. 40, ra. 19, W. 5th mer.). Cairn formation.
15. South side of Isaac Creek at Sawtooth Mountain, Jasper National Park. Cairn formation.
16. At headwaters of an unnamed northern tributary to the Bighorn River (sec. 27, tp. 39., ra. 19, W. 5th mer.). Lower Flume formation.
17. North side of the valley of Little Elbow River at Mount Remus (sec. 24, tp. 21, ra. 8, W. 5th mer.). In a fault slice of the Cairn formation.

    17A. Lower 200 ft. of Cairn formation at this locality.
18. Headwaters of Wasootch Creek on slopes of Mount MacDougall (sec. 28, tp. 22, ra. 8 W. 5th mer.). Cairn formation.
19. One mile north of North Ram River, 4 miles west of Onion Lake (lat. 52°8′ N., long. 116° 18′ W.). 110–120 feet above base of Flume formation.
20. On south side of Mt. Fox above Elk Lakes, British Columbia near the Alberta border. Costigan member of Palliser formation.
21. On south side of Mt. Broadwood, 16 miles south of Fernie, British Columbia. Argillaceous limestone equivalent to Fairholme group.
22. Two miles north of Clearwater River, Second Range of Rockies (lat. 51°54′ N., long. 115°56′ W.). Flume formation, 47 feet above base.

    22A 210–220 feet above base of Flume formation at this locality.
23. Mount Dalhousie, Front Range (lat. 52°38′ N., long. 116°57′ W.). 180–190 feet below top of Southesk formation Arcs member.
24. North side of Panther River at Front Range (lat. 51°37′ N., long. 115°26′ W.). 117–127 feet above base of Cairn formation.
25. Headwaters of a small creek flowing northwest into Job Creek near its junction with the Brazeau River (lat. 52°26′ N., long. 116°41′ W.). 282–283 feet above base of Cairn formation.

    25A. Uppermost Cairn formation at same locality.

    25B. 60–70 feet above base of the Alexo formation at the same locality.

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MANUSCRIPT RECEIVED MAY 15, 1960

EXPLANATION OF PLATE 107

All figures magnified 10 times unless otherwise indicated.

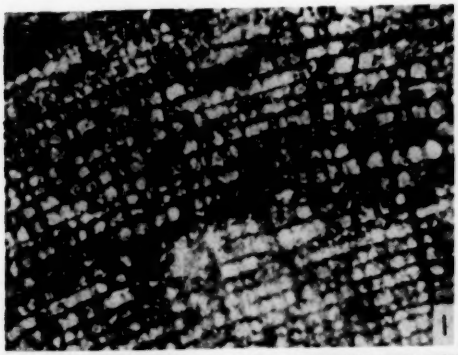
FIGS. *1–3*—*Trupetostroma tenue*, n. sp. *1*, vertical section of holotype (G.S.C. 15,322) showing persistent laminae and superposed pillars. Locality 7. *2*, tangential section of holotype; *3*, vertical section of holotype (×40) showing the thin, spreading pillars with some vacuoles at the top, and their imperfect superposition.

4,5—*Ferestromatopora jacquensis* Galloway. *4*, vertical section (G.S.C. 15,323) showing central zones of regular structure and marginal zones of irregular structure; *5*, tangential section of same specimen. Locality 22A.

6—*Stromatopora* cf. *cooperi*, Lecompte. Vertical section of a specimen (G.S.C. 15,324) with regular structure and many fewer astrorhizal canals than usual. Locality 14.

7,8—*Clathrocoilona* cf. *spissa* Lecompte. *7*, Vertical section of a specimen (G.S.C. 15,325) showing a comparatively regular part of the structure; *8*, tangential section of the same specimen. Locality 12.

9,10—*Amphipora ramosa* (Phillips), *9*, cross section of a specimen (G.S.C. 15,326) which shows features typical the the species. Locality 25A. *10*, cross and axial sections of a variant with wide axial canal and no marginal cysts, which resembles *A. laxeperforata* Lecompte. Locality unknown but from Flume formation. (G.S.C. 15,327)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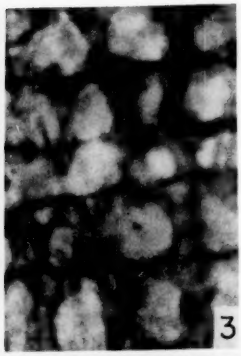
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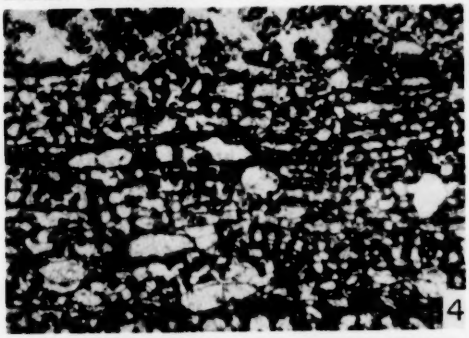
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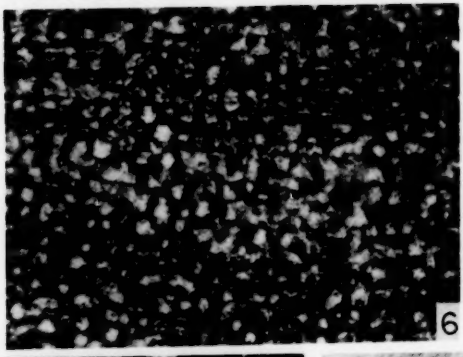
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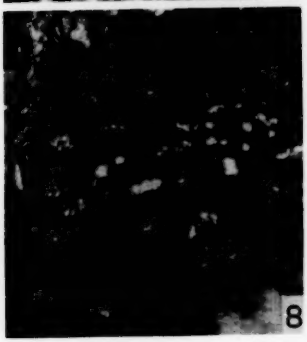
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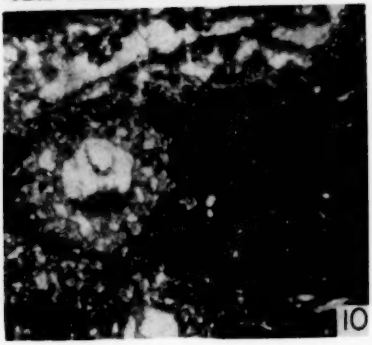
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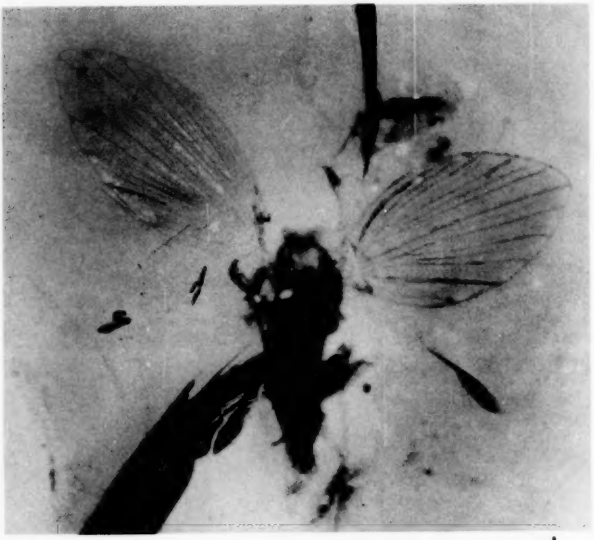

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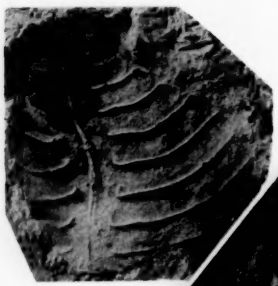

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JOURNAL OF PALEONTOLOGY, V. 35, NO. 5, P. 949–951, PL. 108, 3 TEXT-FIGS., SEPTEMBER, 1961

FOSSIL PSYCHODIDAE (DIPTERA: INSECTA) IN MEXICAN AMBER; PART I

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ABSTRACT—Two psychodid flies are recorded as the first fossil members of this family in the western hemisphere. *Trichomyia antiquaria* and *Brunettia hurdi* are described from the late Oligocene amber of the Simojovel area, Chiapas, Mexico.

THE discovery of two fossil Psychodidae in amber from Chiapas, Mexico, constitutes the first fossil record of members of this family in the western hemisphere. Other fossil psychodids have been found, but these have been largely in Baltic amber from Europe (see Meunier, 1905, Ann. Musei Nationalis Hungarici, *3*:235–255). The Chiapas specimens were embedded in amber of late Oligocene or early Miocene age and are referable to modern genera. One of them belongs to the genus *Trichomyia*, which is fairly well represented by fossil specimens elsewhere and apparently was more abundant during the Tertiary than at present. The other Mexican specimen is a member of *Brunettia* and is the most significant of the two individuals. At present *Brunettia* is primarily an Indo-Malayan genus and is well represented in the Oriental and Ethiopian regions, but only two species are known from North America. The Mexican fossil *Brunettia* indicates that the genus was more widespread during the middle Tertiary than it is now. It also shows that the genus at that time had reached approximately the level of development at which it stands today.

TRICHOMYIA ANTIQUARIA Quate, n. sp.
Text-figs. 1,2; pl. 108, fig. 2

Male.—Antenna (text-fig. 1) with flagellar segments elongate pyriform, basal two-thirds covered with hairs, distal third bare, sensory filaments sinuous, little longer than segments bearing them. Wing with venation much like that of *T. urbica* (Curtis) (type of the genus), Sc ending little beyond base of R_{2+3}, Cu ending little distad of medial fork. Male genitalia (text-fig. 2) with dististyle apparently slender and bearing long spine at apex; dististyle apparently artificially bent as shown in illustration; structure of aedeagus not visible; surstyle with sparse covering of hairs, rather long and tapering from base to apex, apex truncate, about twelve bristles at apex.

Holotype ♂, Univ. Calif. Mus. Paleo. no. 12685, loc. B-5103.

This fossil psychodid is clearly assigned to the genus *Trichomyia* on the basis of the structure of the antennae and the wing venation, both of which are quite visible, though the wings are folded. The coxites and surstyle of the male genitalia are unlike any contemporary *Trichomyia* with which I am

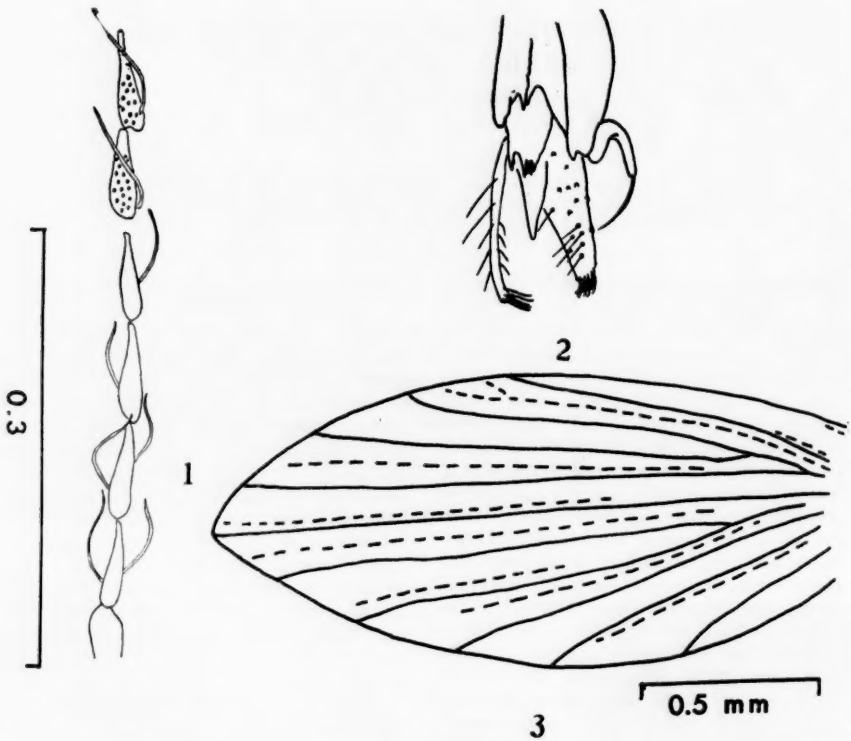
EXPLANATION OF PLATE 108

FIG. *1*—*Brunettia hurdi* Quate, n. sp. Ventral view of holotype ♀ (Univ. Calif. Mus. Paleo. No. 12671).

2—*Trichomyia antiquaria* Quate, n. sp. Lateral view of holotype ♂ (Univ. Calif. Mus. Paleo. No. 12685).

3–5—*Leptodus* sp. *3,4*, latex replica of interior of pedicle valve, ×1, and natural mold from which replica was made, ×2 (USNM 139060a, from USGS loc. 18577-PC). *5*, natural mold of pedicle valve interior, another specimen, ×1 (USNM 139060b, from USGS loc. 18577-PC).

6—*Leptodus* aff. *L. nobilis* (Waagen). Fragmentary pedicle valve, ×1 (USNM 139061, from USGS loc. 3945—green).



TEXT-FIGS. *1,2*—*Trichomyia antiquaria* Quate, n. sp. *1*, antenna, pedicel and flagellar segments 1 to 7; *2*, male genitalia, dorsal view.

TEXT-FIG. *3*—***Brunettia hurdi*** Quate, n. sp., wing of female: broken lines indicate folds in the wing membrane.

acquainted. The spine at the tip of the dististyle and the cluster of spines at the apex of the surstyle are distinct. *Trichomyia brochata* from Madagascar (Quate, 1957, Nat. Malgache, *9*:252) has a cluster of spines on the surstyle, but otherwise is entirely dissimilar to *antiquaria*.

Trichomyia is apparently an ancient genus of psychodids. There are only 22 species known today, but they are widely distributed over the earth and most are not closely related to each other judging from the diverse structures of the male genitalia. Species of the genus are known from all the zoogeographic regions, except the Oriental, including the Hawaiian Islands and Micronesia.

BRUNETTIA HURDI Quate, n. sp.
Text-fig. 3; pl. 108, fig. 1

Female.—Eyes with eye bridges converging about antennae, flagellar segments distorted but apparently elongate pyriform; wing (text-fig. 3) with forks near base of wing, R_5 ending just at apex, few hairs visible, but no scales. Cerci elongate triangular with rounded apices. Other structures not visible. Wing length about 2.0 mm.

Holotype ♀, Univ. Calif. Mus. Paleo. no. 12671, loc. B-5103.

On the basis of the wing venation, which is clearly visible, this specimen is a member of the genus *Brunettia*, not unlike a number of modern species with the pectinate radial

sector, the forks close to the base of the wing and the moderately broad wing in the female (males have much broader wings).

This is the first fossil record of the genis *Brunettia* and also the first Neotropical record of the genus. There are 33 species of the genus known (but a number of undescribed Indo-Malayan species await further study), and all but two are either Ethiopian or Oriental in distribution. Two species, *B. nitida* (Banks) and *sycophanta* Quate, are known from North America. None have been described from Central or South America prior to this report.

I take pleasure in dedicating this species to Dr. Paul D. Hurd, Jr. in recognition of his contribution to paleontology through his work in Mexico.

Both specimens were in amber from locality B-5103, Las Cruces landslide, Chiapas, México. The locality is about 23 kms (airline) south of east from the town of Simojovel and about 6.8 kms southeast of the headquarters of the Rancho Santo Domingo. The landslide is on the south slope, near the southeast end of the major ridge known locally as Nichalan (also as Cerro Balumtun), and about 1.4 kms northwest of Rancho San José Buena Vista. The amber was found in sandstone exposed near the base of the western edge of the slide. The marine invertebrate fauna from the adjacent beds indicates an age in the range from late Oligocene to early Miocene.

ACKNOWLEDGMENTS

Acknowledgment is made to the Associates in Tropical Biogeography of the University of California who have supported the field explorations and acquisition of the Chiapas amber, and to J. Wyatt Durham of the Museum of Paleontology, and P. D. Hurd, Jr. and Ray F. Smith of the Department of Entomology and Parasitology, University of California, who have made this fossil material available for study.

JOURNAL OF PALEONTOLOGY, V. 35, NO. 5, P. 952–954, PL. 108, SEPTEMBER, 1961

NEW OCCURRENCES OF *LEPTODUS* (BRACHIOPODA) IN THE PERMIAN OF THE WESTERN UNITED STATES[1]

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ABSTRACT—Isolated unattached specimens of the reef dwelling brachiopod *Leptodus* collected from the Phosphoria formation in southwestern Montana and the Robinson formation in northern California are described as *Leptodus* sp. and *L.* aff. *L. nobilis* (Waagen) respectively.

OVER the years, paleontologists have paid considerable attention to the leptodid brachiopods because of the peculiar nature of their brachial valve and the implied environmental significance of their occurrence. The brachial valve (or plate) with its transverse loops and the pedicle valve, with ridges which fit between the loops of the opposite valve, comprise a distinctive shell that is easy to recognize in late Paleozoic collections of fossils.

In the west Texas Permian, abundant leptodids apparently grew together in relatively shallow water in banks and reefs, much like the oysters in our present day seas. The rarity of leptodids in rocks beyond the Delaware Basin probably reflects unfavorable local environments. Two previous reports of such leptodids in western North America are from the Cache Creek group in British Columbia (Kindle, 1926) and from the Coyote Butte formation in central Oregon (Cooper, 1957, p. 26).

It is of some interest, therefore, to record *Leptodus* in a dolomitic siltstone near the top of the Phosphoria formation in southwestern Montana and in the volcanic-rich sedimentary rocks of the Robinson formation in northern California.

Montana locality.—In 1949, in connection with detailed stratigraphic work in Beaverhead County, Montana, W. R. Record obtained a collection of fossils which included one *Leptodus*. The collection came from a bed 3.4 feet thick, the top of which was considered to be 2.7 feet below the top of the Phosphoria formation (Cressman and others, 1953, p. 10). In the stratigraphic section graphically shown by Cressman (1953, pl. 1), these beds are placed in unit E which is now included in the Tosi chert member of the Phosphoria formation (McKelvey, and others, 1959, p. 30).

The *Leptodus* was first noted by Yochelson during the spring of 1959. Collections from other sections in Montana were examined but no additional specimens were found. In the summer of 1959, E. R. Cressman, E. L. Yochelson and Eli Zohar visited the locality and obtained more than a dozen specimens of *Leptodus* in an hour's collecting.

The locality is readily accessible by car and is most easily reached by taking the unpaved Blacktail Creek Road south and east from Dillon, Montana, to 1.2 miles north of the junction with the Antone Ranger Station Road. The strata are exposed on the east-facing hill slope just a few feet above road level. The fossiliferous beds are light yellow to buff, slightly dolomitic siltstone which weathers in thin irregular slabs coated with limonite. Although the slabs are crowded with fossils, most specimens are poorly preserved, the shell material having been dissolved away and partially replaced by iron and manganese minerals.

The associated fauna includes: *Lingula* sp., *Derbyia* sp., "*Horridonia*" sp., *Wellerella* sp., *Composita* sp., *Hustedia* sp., *Rhynchopora* sp., *Permophorus* sp., *Aviculopecten* sp., and *Acanthopecten* sp. Field observations suggest that the *Leptodus*, *Wellerella*, and *Rhynchopora* are in a relatively narrow zone with most of the productoids and pectenoids occurring just above.

None of the *Leptodus* specimens show attachment to another shell or to a hard substrate although the distorted shapes of the pedicle valves (see Plate 108, figs. 3,4) may reflect the condition of crowding characteristic of the *Leptodus* growth habit. Possibly these reef-dwelling forms were transported to this locality; the abundance of shells in a single stratum is suggestive,

[1] Publication authorized by the Director, U. S. Geological Survey.

though not definite, evidence of transport.

California locality.—Kindle (1926) mentions that G. H. Girty wrote him of an occurrence of *Leptodus* in California. The specimen referred to has been located in the Geological Survey collections and is described and illustrated herein.

During the 1890's and early 1900's, in the course of mapping by J. S. Diller and associates, several collections of fossils were obtained from the Robinson formation near Taylorsville in northern California. Some of these fossils were identified by C. D. Walcott in 1891 (Diller, 1908, p. 27), although the *Leptodus* was not recognized until Girty reexamined the material in 1906.

The collection which includes the *Leptodus* was made in the Genesee Valley, Plumas County, about 7½ miles east of Taylorsville. Diller (1908, p. 27) described the locality as: ". . . chiefly from reddish brown sandstone and tuff on the first spur, about half a mile northwest of the Robinson house." Fossils are mostly preserved as molds, many have been squeezed and distorted, and secondary minerals fill some of the voids.

The associated fauna includes: echinoderm debris, large crinoid columnals, undetermined horn corals, indeterminate fenestrate bryozoans, *Derbyia* sp., *Meekella* sp., *Waagenoconcha?* sp., *Spiriferella?* sp. (an alate form), *Squamularia* sp., *Spiriferina?* sp., *Aviculopecten* sp., *Clavicosta?* sp., *Annuliconcha* sp., and other indeterminate pelecypods.

Leptodus sp.
Pl. 108, figs. 3–5

The material from southwest Montana consists of two fine internal molds of the pedicle valve and a dozen or so fragmentary ones. The general shape of the valve is ostreiform, suggesting accommodation during growth to the substrate to which the shells were attached. The dental areas are small and appear as described by A. Williams (1953, pl. 2, fig. 5). The muscle area is weakly impressed; a thin median axis arises forward of it and continues to the anterior margin. There appears to be a bifurcation, or a depression developed, in the anterior third of the median axis. Lateral ridges are sharp, keel-like, and diverge from the median axis at approximately 90°, curving posteriorly at their outer ends. Eight to ten pairs of ridges are symmetrically arranged about the median axis. Troughs between ridges are broad and flat bottomed. Incomplete specimens measure about 45 mm. long and 40 mm. wide at the broadest part approximately one-third the distance from the anterior margin.

Discussion.—There appears to be no doubt that these specimens represent the genus *Leptodus*, although the material is not so well-preserved as to warrant a new specific name. The shape and size of the valves, as well as the disposition and number of ridges and troughs, are similar to undescribed species from the Word limestones 3 and 4, as used by G. A. Cooper (oral communication, 1960), present in the collections of the U. S. National Museum. *Leptodids* of the same general shape and size are found in beds from the Leonard to the Capitan in west Texas. Thus, the Montana locality cannot be correlated unequivocally with the upper Word by these leptodids alone.

The Montana species is in many respects like that described by Wanner and Sieverts from Timor (1935, p. 242) as *Lyttonia catenata*. The Montana specimens are about the same size as the one described by Kindle (1926) from the Cache Creek group in British Columbia, although Kindle's shell apparently has lateral ridges that are entirely double-keeled. The specimen from California, discussed in this paper, appears to differ from the Montana species in that it is considerably larger. The specimen described by Cooper (1957, p. 26) is probably not a *Leptodus;* it perhaps should be assigned to *Pseudoleptodus* (Stehli, 1956, p. 312) or *Keyserlingina* (Cooper, oral communication, July 1960).

Figured specimens.—Both pedicle interior molds: USNM 139060a; 139060b.

Locality.—(USGS loc. 18577-PC) Montana, Beaverhead County; SE¼, sec. 26, T. 12 S., R. 6 W.; 3–6 ft. below top of Tosi chert member of the Phosphoria formation. Collectors: E. L. Yochelson, E. R. Cressman, E. Zohar, 1959.

Leptodus aff. *L. nobilis* (Waagen)
Pl. 108, fig. 6

A single fragment of a pedicle valve has been collected from the Robinson formation near Taylorsville, California. This clearly represents a large shell, possibly as long as

60 mm. and as wide as 50 mm. Ten pairs of broad lateral ridges diverge at nearly right angles from, and are symmetrically arranged about, the median axis.

Discussion.—In size and shape this specimen most resembles *L. nobilis* (Waagen) described from Permian beds in many parts of the Old World. It is unlike anything known from North America. The Robinson formation has been correlated with the Nosoni and Dakkas in California and is considered to be, at least in part, of Late Permian age. It is also possibly partly equivalent to the Phosphoria of Wyoming, Idaho and Montana.

Figured specimen.—(USGS loc. 3945—old green catalogue) California, Plumas County; Kettle Rock quadrangle, probably SW¼ sec. 3, T 25 N., R. 11 E; from unknown level in Robinson formation. Collector: J. S. Diller, 1891.

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EXPLANATION OF PLATE 108

FIG. *1*—*Brunettia hurdi* Quate, n. sp. Ventral view of holotype ♀ (Univ. Calif. Mus. Paleo. No. 12671).

2—*Trichomyia antiquaria* Quate, n. sp. Lateral view of holotype ♂ (Univ. Calif. Mus. Paleo. No. 12685).

3–5—*Leptodus* sp. *3,4*, latex replica of interior of pedicle valve, ×1, and natural mold from which replica was made, ×2 (USNM 139060a, from USGS loc. 18577-PC). *5*, natural mold of pedicle valve interior, another specimen, ×1 (USNM 139060b, from USGS loc. 18577-PC).

6—*Leptodus* aff. *L. nobilis* (Waagen). Fragmentary pedicle valve, ×1 (USNM 139061, from USGS loc. 3945—green).

JOURNAL OF PALEONTOLOGY, V. 35, NO. 5, P. 955–962, PL. 109–110, 3 TEXT-FIGS., SEPTEMBER, 1961

THE STRATIGRAPHIC OCCURRENCE OF SOME LOWER MISSISSIPPIAN CORALS FROM NEW MEXICO AND MISSOURI[1]

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ABSTRACT—The *Cleistopora typa gorbyi* faunule, characterized by *C. typa gorbyi* and *Microcyclus blairi*, is of earliest Mississippian age and is present in the Caballero formation of New Mexico, and the Compton limestone and the Sedalia dolomite (in part) in Missouri. The Northview shale fauna from the lower part of the Northview shale in the Northview basin may be in part the equivalent of the *C. typa gorbyi* faunule.

The *Cleistopora typa typa* faunule, characterized by *C. typa typa*, *C. placenta*, *Homalophyllites calceolus*, *Vesiculophyllum sedaliense*, *Lithostrotionella microstyla*, and *Michelinia expansa*, overlies the *C. typa gorbyi* faunule in New Mexico and Missouri. The stratigraphic units of Early Mississippian age in New Mexico are laterally persistent, and the coral faunules are sharply confined to certian parts of the section. The coral zonation is not as obvious in Missouri where the Compton limestone and the Sedalia dolomite interfinger, and the Northview shale and the Sedalia dolomite interfinger. The *C. typa typa* faunule occurs in the top of the Sedalia dolomite (in part), the top of the Northview shale, and the Pierson limestone. It is found in the Andrecito and perhaps in the Alamogordo members of the Lake Valley formation in New Mexico. The faunule is Early Mississippian in age and younger than the *Cleistopora typa gorbyi* faunule. In the Northview basin the *C. typa typa* faunule is replaced, at least in part, by a molluscan assemblage which occurs with *Scalarituba* and *Taonurus*. In New Mexico, elements of the *C. typa typa* faunule occur with *Scalarituba* and *Taonurus*.

The corals of the older *C. typa gorbyi* faunule are minor elements in a dominantly brachiopod-rich assemblage. On the other hand, corals of the younger *C. typa typa* faunule are a conspicuous part of the total fossil assemblage. The *C. typa typa* faunule is widespread in the United States, but the *C. typa gorbyi* faunule is more restricted geographically.

INTRODUCTION

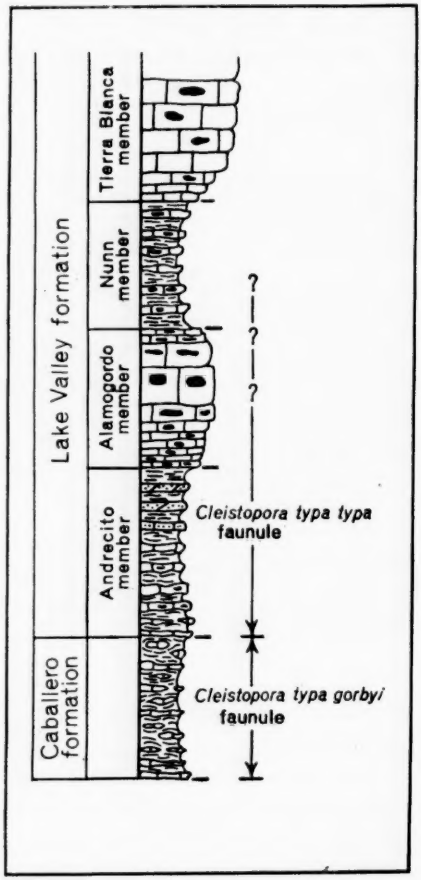
THE purpose of this paper is to point out some corals that are present in New Mexico and Missouri in the lower part of the Mississippian system and to discuss their distribution in the light of present knowledge. The corals discussed are easily recognized and are useful to one who is not a coral specialist. They are by no means the only corals found in these rocks.

Some of these corals were recently described by R. M. Jeffords (1955) from Mississippian rocks of New Mexico. Specimens furnished Jeffords by L. R. Laudon and me for his study were inadequately documented as to geographic distribution and stratigraphic range because we had collected them prior to 1946 during the early part of our investigations of Mississippian rocks in New Mexico. Since then we have together and separately visited many additional localities and collected many corals as yet unstudied by a coral specialist. In addition, I have since examined many localities of lower Mississippian rocks in Missouri. Observations made in the later studies indicate that certain corals occur in assemblages that are useful in stratigraphic studies. Much work remains to be done before the full details of these faunules can be outlined, but coral species and genera characteristic of the *C. typa typa* faunule occur in the lower Mississippian rocks at many places in the United States, and forms characteristic of the *C. typa gorbyi* faunule are found at many localities in the Mississippi Valley region as well as in New Mexico.

STRATIGRAPHY

Discussion of the stratigraphic relations of the rocks in which the corals occur is a necessary prelude to comments on their distribution and age significance. This is especially true for Early Mississippian rocks in southwestern Missouri.

[1] Publication authorized by Sinclair Oil & Gas Company.

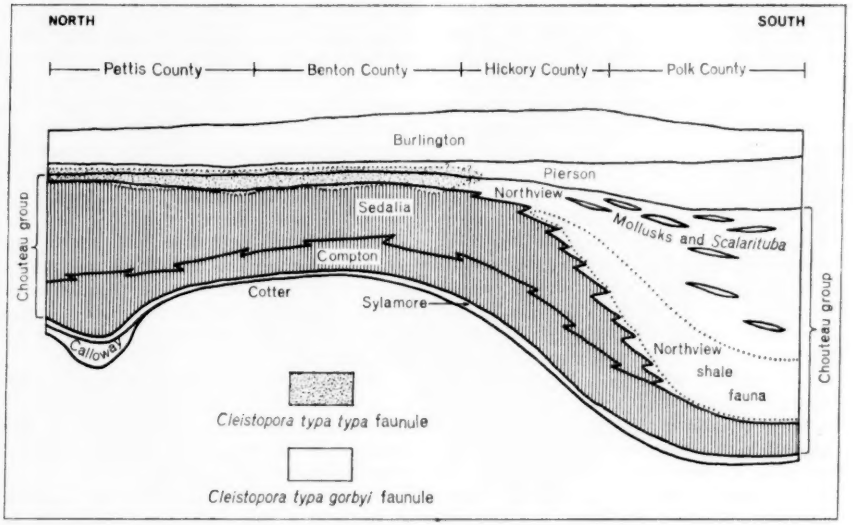


TEXT-FIG. 1—Caballero Formation and Lake Valley formation (in part) in southern New Mexico showing distribution of the coral faunules (modified after Laudon and Bowsher, 1949).

New Mexico.—The stratigraphic names used by Laudon and Bowsher (1941 and 1949) for Lower Mississippian rocks of southern New Mexico are followed in this report. The corals discussed herein are found in the Caballero and the lower part of the Lake Valley formation, including the Andrecito member, probably the Alamogordo member, and, perhaps, the lower part of the Nunn member of the latter (see text-fig. 1). Bioherms and related facies in the lower part of the Lake Valley formation alter the normal stratigraphic succession in a few places. However, over most of the area of exposure in southern New Mexico (Laudon and Bowsher, 1949, p. 12), the members are laterally persistent and easily recognized. Because of this simple stratigraphic framework it is relatively easy to determine the relations of faunal zones and rock units. The large area of exposure, lateral persistence of rock units, and abundant fossils make this area important in the study of Early Mississippian faunas.

Missouri.—Rapid facies changes characterize the Lower Mississippian strata beneath the Burlington limestone in southwestern Missouri. The term Chouteau (Swallow, 1855, p. 101) is the first stratigraphic name published for any of these strata. Although other stratigraphic names were proposed for some of the rock units beneath the Burlington limestone, the term Chouteau has been retained by many workers. The varied use of the name in stratigraphic classifications has rendered the term ambiguous. The stratigraphic classifications of previous workers are discussed by Beveridge (1951) and Beveridge and Clark (1952). The classification proposed by Beveridge and Clark (1952) is followed in this report because my field observations in the area concerned accord closely with those of Beveridge and Clark (text-fig. 2).

The Compton limestone, a cream-colored, semilithographic, nodular limestone with intercalated shale, named by Moore (1928, p. 118), is the basal unit of the Chouteau group of Beveridge and Clark (1952). The Sedalia limestone, named by Moore (1928, p. 78 and 89), is really a siliceous dolomite in southwestern Missouri where it conformably overlies or interfingers laterally with the upper part of the Compton limestone (Beveridge and Clark, 1952). The Sedalia dolomite of Beveridge and Clark is well developed in the vicinity of Sedalia, Missouri. Eastward it is replaced by the upper part of the Compton limestone, which makes up the entire Chouteau group near Columbia, Missouri. Southward in the Northview Basin (Beveridge and Clark, 1952, p. 14–15) it is replaced by the Northview shale of



TEXT-FIG. 2—General outline of facies in the Chouteau group (modified after Beveridge and Clark, 1952) and the distribution of coral faunules.

Weller (1901, p. 140) (see fig. 2). Along the northern edge of this basin the Northview shale is represented by 3 to 10 feet of shale lying on top of the Sedalia dolomite. This thin wedge of Northview shale can be observed just above the Sedalia dolomite in exposures through Benton and Pettis counties. A typical exposure can be examined at Kaiser's locality 57 (1950, p. 2145) in the NE $\frac{1}{4}$ of Section 8, Township 38 North, Range 24 West, $\frac{3}{4}$ mile northeast of Corbin, St. Clair County, Missouri.

Dolomitic silstone lenses are common in the Northview shale in Polk County. The Northview shale is overlain by the Pierson limestone of Weller (1901, p. 140) which is a brown dolomite. Northward in Benton and Pettis counties this dolomite becomes increasingly crinoidal. Locally, crinoid fragments are so abundant that the formation is difficult to distinguish from the overlying crinoidal limestone of the Burlington. Eastward, near Columbia, Missouri, brown dolomitic, crinoidal limestone beds in the basal few feet of the Burlington limestone apper to represent the Pierson limestone of southwestern Missouri.

STRATIGRAPHIC DISTRIBUTION OF THE CORAL FAUNULES

Two coral faunules are present in the strata discussed above. The *Cleistopora typa gorbyi* faunule is the older one and directly underlies the *Cleistopora typa typa* faunule which is more widespread.

CLEISTOPORA TYPA GORBYI *faunule.*—*Leptopora gorbyi* Miller, 1891, referred to as *Cleistopora typa gorbyi* (Miller) n. comb. by Jeffords (1955, p. 6–8), and *Microcyclus blairi* Miller, 1891 (Jeffords, 1955, p. 3–4), are common in the Compton limestone of Missouri and the Caballero formations in New Mexico (Laudon and Bowsher, 1941 and 1949). Although conspicuous in the two formations, they are subordinate elements in a brachiopod-rich fauna. For the purpose of this paper, I shall refer to *C. typa gorbyi* and *M. blairi* as composing the *C. typa gorbyi* faunule. Although *C. typa gorbyi* is essentially restricted to the Chouteau group and the Caballero formation, *M. blairi* at a few places ranges upward into the overlying units. However, the occurrence of the two together is significant.

It is beyond the scope of this paper to

discuss all the fossils that occur with this faunule, but nearly all of the crinoids (Peck and Keyte, 1938, p. 70–108) of the Chouteau of Swallow (1855), and most of the brachiopods (Branson, 1938) of the Chouteau of Swallow (1855) occur with the *C. typa gorbyi* faunule.

In the base of the Caballero formation, specimens of *C. typa gorbyi* (pl. 109, fig. 1a,b) are small and have a central corallite surrounded by a single circlet of from four to seven corallites. The coralla are essentially flat and the corallites have very thin walls. Upward in the formation the colonies become larger and more massive. Many exhibit an incomplete second circlet of corallites. Specimens from the top part of the Caballero approach *C. typa typa* morphologically. Coralla of *M. blairi* (pl. 110, fig. 1a,b and 2a,b) are commonly very small and very thin. *M. blairi* also occurs sparingly in the lower part of the overlying Lake Valley formation (Laudon and Bowsher, 1941 and 1949).

These two coral species are abundant in the Compton limestone fauna in Missouri. However, the gradual change in *C. typa gorbyi* upward in the section is less conspicuous in the Compton limestone because variation within a single collection from any particular level is great. In Missouri, *C. typa gorbyi* occurs throughout the Compton limestone and at some localities appears all through the overlying Sedalia dolomite. Specimens of *M. blairi* are thin and small in the Comptom and overlying Sedalia in Missouri. Fossils, including these corals, are not abundant in the Sedalia. The *C. typa gorbyi* faunule appears to be missing from the very top of the Sedalia dolomite in some areas, having been replaced by the *C. typa typa* faunule.

The exact time relationships between the *C. typa gorbyi* faunule and the Northview shale fauna (see fig. 2), which occurs in the base of the Northview shale in the Northview Basin, are not known.

In summary, the *C. typa gorbyi* faunule characterizes the Caballero formation in New Mexico (Laudon and Bowsher, 1941 and 1949) and the Compton limestone and Sedalia dolomite in Missouri (Beveridge and

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EXPLANATION OF PLATE 109

FIG. *1*—*Cleistopora typa gorbyi* (White). Caballero Formation, north side of Alamo Canyon, SE¼ SW¼ sec. 24, T. 16 S., R. 10E., Lincoln County, New Mexico (U. S. Natl. Mus. Loc. 3046). *1a*, upper surface, ×2; *1b*, base, ×2.

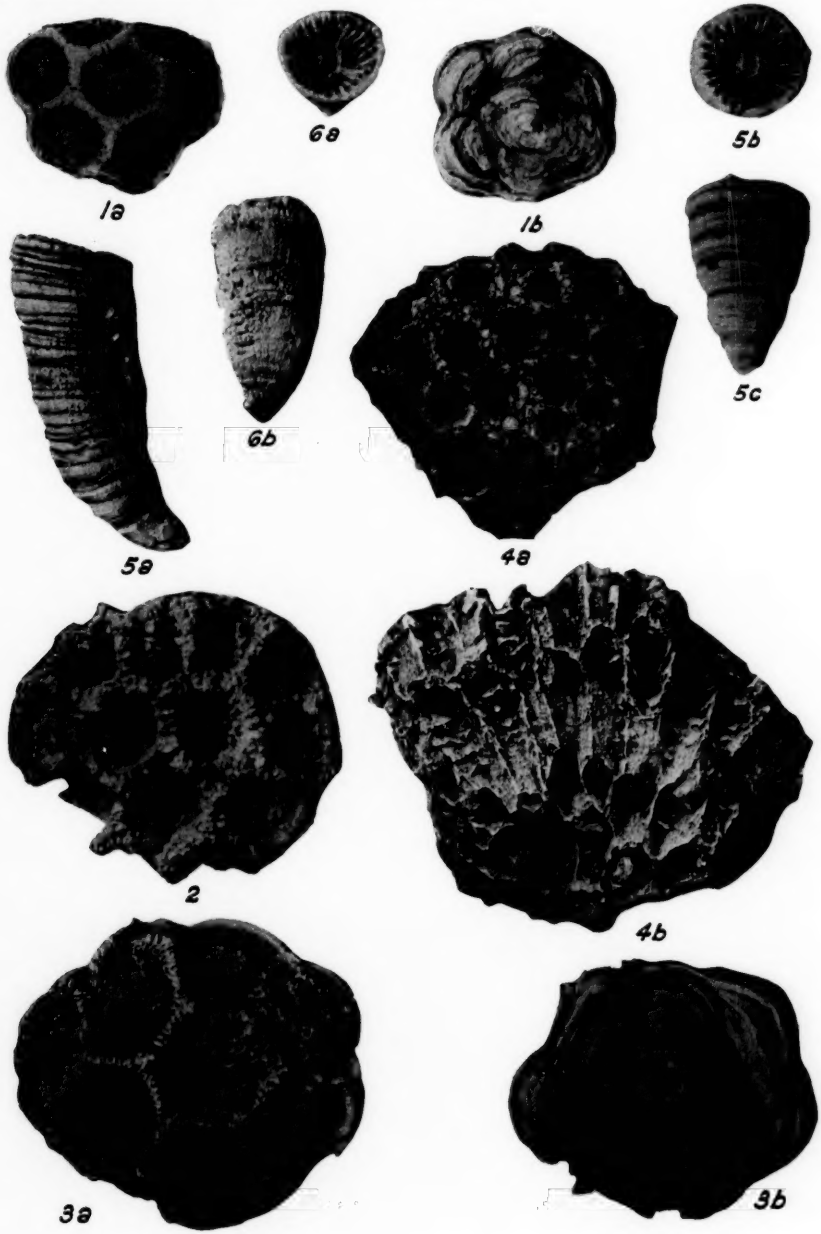
2—*Cleistopora typa typa* (Winchell). Andrecito member, Lake Valley Formation, NE¼ SW¼ sec. 23, T. 16 S., R. 10 E., Lincoln County, New Mexico (U. S. Natl. Mus. Loc. 3020). Upper surface of a silicified specimen freed from limestone matrix by use of hydrochloric acid.

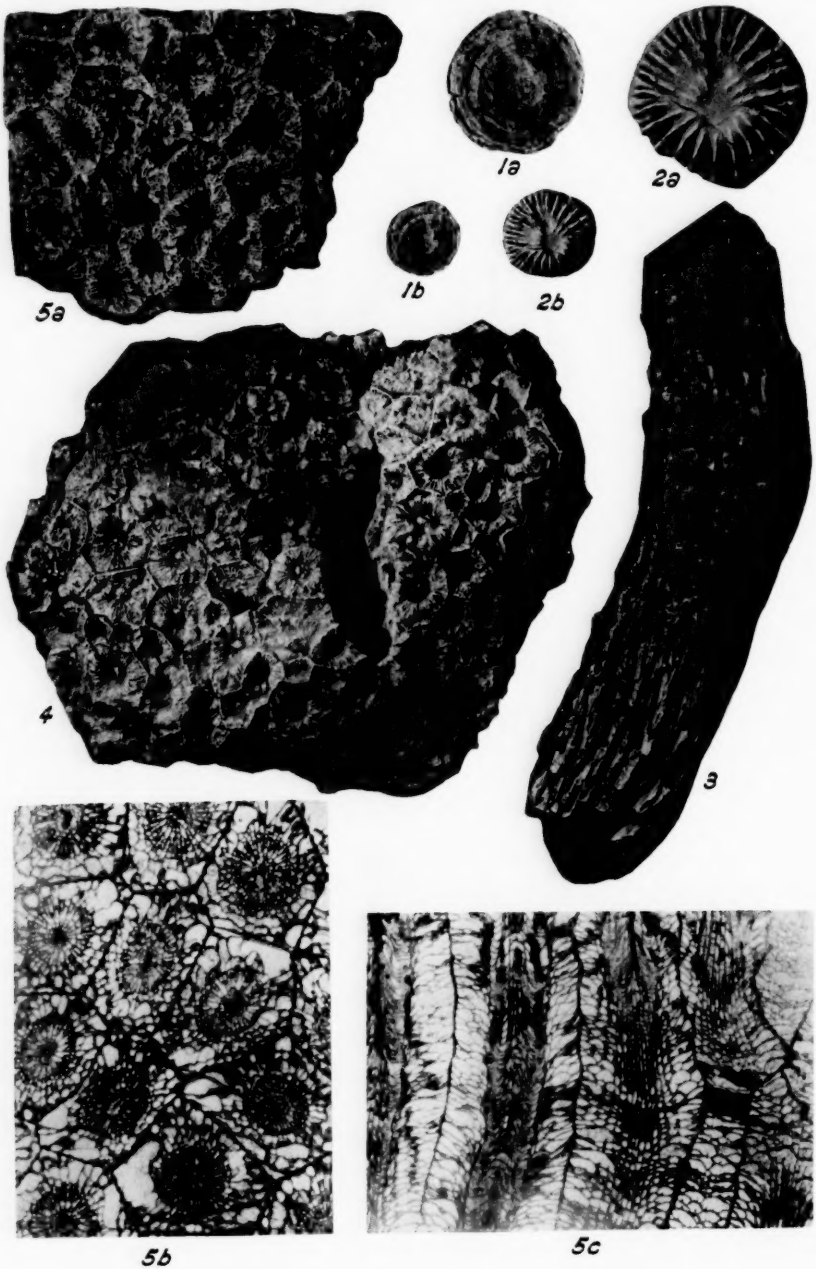
3—*Cleistopora typa typa* (Winchell). Northview shale, from north side of the road, northeast side of hill, northeast of Corbin, NE¼ sec. 8, T. 38 N., R. 24 W., St. Clair County, Missouri (U. S. Natl. Mus. Loc. 3287; Kaiser, 1950, fig. 3b.). *3a*, upper surface, ×2; *3b*, base of a second specimen, ×2.

4—*Michelinia expansa* White. Northview shale, from the north side of the road, northeast side of hill, northeast of Corbin, NE¼ sec. 8, T. 38 N., R. 24 W., St. Clair County, Missouri (U. S. Natl. Mus. Loc. 3287; Kaiser, 1950, fig. 3b). *4a*, upper surface showing cystose dissepiments, ×1; *4b*, view of the base of another specimen from which the epitheca is eroded showing flat tabulae and cystose dissepiments, ×1.

5—*Homalophyllites calceolus* (White). Top 2 feet of Sedalia dolomite and overlying Northview shale, 1½ mi. east of Gerster, center east line, SW¼ NW¼ SE¼ sec. 22, T. 37 N., R. 24 W., St. Clair County, Missouri. *5a*, side view of a large specimen showing constrictions, ×2; *5b*, calyx of another specimen, ×2; *5c*, cardinal view of specimen in *5b*, ×2.

6—*Homalophyllites calceolus* (White). Andrecito member, Lake Valley Formation, 3 mi. north of Lake Valley, SE¼ NE¼ SW¼ sec. 10, T. 18 S., R. 7 W., Sierra County, New Mexico. *6a*, calyx of specimen freed from limestone matrix by use of hydrochloric acid, ×2; *6b*, cardinal view of specimen in *6a*, ×2.


1a
6a
1b
5b
6b
5c
5a
4a
2
4b
3a
3b

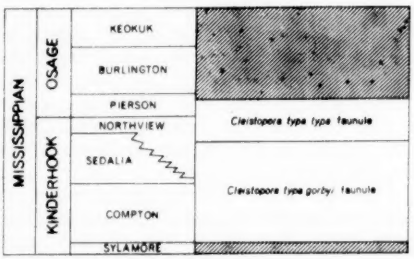

1a
2a
1b
2b
5a
4
3
5b
5c

Clark, 1952), except for the top part of the Sedalia in some areas. These species of corals along with numerous other fossils from the Compton limestone represent a distinct and widespread assemblage of earliest Mississippian age.

CLEISTOPORA TYPA TYPA *faunule.*—*Leptopora typa* Winchell, 1863, referred to as *Cleistopora typa typa* (Winchell) n. comb. (pl. 109, fig. 2 and 3a,b) by Jeffords (1955, p. 7), occurs in the upper part of the Northview shale and the Pierson limestone in the Osceola, Missouri, area, along with *Vesiculophyllum sedaliense* (White) (see pl. 110, fig. 3), *Lithostrotionella microstyla* (White) (see pl. 110, fig. 4), *Cleistopora placenta* (White), *Michelinia expansa* White (see pl. 109, figs. 4a,b), and *Homalophyllites calceolus* (White) (see pl. 109, figs. 5a–c). For the purpose of this discussion I shall refer to these corals as constituting the *C. typa typa* faunule.

White (1880, p. 159) in discussing the occurrence of *L. microstyla* remarked,

"It is also an interesting fact that these corals occupy a very narrow horizon at the top of the Kinderhook division, just beneath the Burlington limestone, and that in all remainder of the Kinderhook division corals are rare, if not altogether absent. This coral horizon seems to be a well-marked one; and from the fact that the only corals which have yet been found in that division in Iowa and Illinois occupy an exactly similar horizon with that here referred to in Missouri, it will probably prove to be one of considerable geographic extent. Up to this time the following ten species of corals have been found in that horizon in Missouri, Iowa, and Illinois: *Zaphrentis calceola* and *Z. acuta* White & Whitfield; *Z. elliptica* White; *Chonophyllum sedaliense* n. s.; *Syringopora harveyi* White; *Favosites* (*Michilinia?*) [*sic*] *divergens* White & Whitfield; *Michilinia* [*sic*] *placenta* n. s.; *M. expansa* n. s.; *Lepidopora* [*sic*] *typa* Winchell; and *Lithostrotion microstylum* n. s."



TEXT-FIG. *3*—Relationships between rock units in Missouri (after Beveridge and Clark, 1952) and the coral faunules.

This highly significant observation by White seems to have been ignored by most workers. Recognition of this fact, however, is fundamental in clarification of the faunal ambiguity which has resulted since 1880.

EXPLANATION OF PLATE 110

FIG. *1*—*Microcyclus blairi* Miller. Caballero Formation, NE¼ sec. 18, T. 17S., R. 11 E., Pig Canyon, Sacramento Mountains, Otero County, New Mexico (specimen U. S. Natl. Mus. no. 135423). *1a*, basal view, ×2; *1b*, basal view, ×1.

2—*Microcyclus blairi* Miller. Caballero Formation, 3½ mi. east of north edge of Alamogordo, NE¼ sec. 14, T. 16 S., R. 10 E., (U. S. Natl. Mus. Loc. 506g, specimen no. 135423). *2a*, calyx, ×2. *2b*, calyx, ×1.

3—*Vesiculophyllum sedaliense* (White). Northview shale, from north side of road, northeast side of hill, northeast of Corbin, NE¼ sec. 8, T. 38 N., R. 24 W., St. Clair County, Missouri (U. S. Natl. Mus. Loc. 3287; Kaiser, 1950, fig. 3b). Side view of a decorticated specimen; most specimens are decorticated.

4—*Lithostrotionella microstyla* (White). Northview shale, from north side of road, northeast side of hill, northeast of Corbin, NE¼ sec. 8, T. 38 N., R. 24 W., St. Clair County, Missouri, (U. S. Natl. Mus. Loc. 3287; Kaiser, 1950, fig. 3b).

5—*Lithostrotionella microstyla* (White). Andrecito member, Lake Valley Formation, from east facing ledge, 50 yards north of New Mexico highway No. 180, 3 mi. east of Santa Rita, NE¼ sec. 20, T. 17 S., R. 11 W., Grant County, New Mexico, *5a*, view of corallum, ×1; *5b*, transverse thin section of specimen in *5a*, ×2; *5c*, longitudinal thin section of specimen in *5a*, ×2.

Workers have failed to differentiate elements of this faunule from those of the underlying *C. typa gorbyi* faunule when describing fossils from the so-called Chouteau of Swallow (1855), a term which has been used for more than seventy years (Branson, 1938) to include all pre-Burlington Mississippian rocks in Missouri.

The distinctive *C. typa typa* faunule has a limited geographic and stratigraphic distribution in Missouri. Species of this faunule are rare, if present at all, south of the Weaubleau quadrangle in St. Clair County where the upper part of the Northview shale carries *Scalarituba*, *Taonurus* and an associated invertebrate assemblage described by Weller (1899). Only a single coral specimen from Polk County is listed from the fauna of the Pierson discussed by Weller (1901, p. 145). However, from the Weaubleau quadrangle northward through Pettis County, where the Northview shale is thin, the corals are abundant in the Northview shale and the Pierson limestone, and at some localities in the top of the Sedalia dolomite. Important localities are in the vicinity of Sedalia, Missouri; near Warsaw, Missouri, at locality 57 of Kaiser (1950, p. 2145); and near Gerster in the Weaubleau quadrangle (Beveridge, 1951).

Cleistopora typa typa is common in the Andrecito member of the Lake Valley formation in the Sacramento Mountains, in the central part of the San Andres Mountains, in the Cooks Range, and in the Kingston, Hillsboro, and Lake Valley areas of New Mexico. *Lithostrotionella microstyla* has been found near Santa Rita, at Bear Mountain near Silver City, and in the Cooks Range. *Homalophyllites calceolus* is present in the Silver City and Hillsboro areas. *Michelinia expansa* and *Vesiculophyllum sedaliense* are undoubtedly present in New Mexico but have not been positively identified.

GEOGRAPHIC DISTRIBUTION OF THE CORAL FAUNULES

The distinctive *Cleistopora typa typa* faunule is conspicuous in New Mexico and Missouri. Species listed by Laudon (1931, p. 426–429) from the Maynes Creek member of the Hampton formation of Laudon (1931, not Campbell, 1899) at LeGrand, Iowa, may belong to this faunule. Species belonging to this faunule are reported by Easton (1944) from the Kinderhook of Illinois. Some elements of the faunule are known from the Mississippian rocks of Ohio. Corals described by Easton and Gutschick (1953) from the Redwall limestone of Arizona apparently include species that may belong to the *C. typa typa* faunule. I have collected what I believe to be *Lithostrotionella microstyla* from the lower part of the Escabrosa limestone near Paradise, Arizona. Helen Duncan (personal communication, 1955) informs me that the assemblage of genera and certain species of the *C. typa typa* faunule as delineated in this paper, occur in the Madison limestone and its equivalents at many places in the Rocky Mountains and the Great Basin. It appears, therefore, that this distinctive coral association, which has for so long remained virtually unnoticed because of the idiosyncrasies of descriptive paleontologic writing, is present in lower Mississippian rocks over a large part of the United States, In addition, Easton (1958) has described this faunule from Mexico.

The older *C. typa gorbyi* faunule probably has a fairly wide geographic distribution, but it is not as readily recognized because of its smaller number of easily identified coral species. However, the total number of species of invertebrate fossils that occur with the older faunule is far greater than the number of species typically associated with the *C. typa typa* faunule.

AGE OF THE CORAL FAUNULES

The *C. typa gorbyi* and the *C. typa typa* faunules are Early Mississippian in age. The *C. typa gorbyi* faunule characterizes the Compton limestone of Missouri and the Caballero formation of New Mexico. It extends upward into the Sedalia dolomite of Missouri. The faunule also occurs in the type section of the Kinderhook in Illinois. Since this faunule is restricted to rocks that all workers class as Kinderhook in age, there is no question about its age significance.

It is not so easy to determine the age of the overlying *C. typa typa* faunule. White (1880, p. 159) considered this faunule to ". . . occupy a very narrow horizon at the top of the Kinderhook division. . . ." The *C. typa typa* faunule ranges from the top

beds of the Sedalia dolomite through the upper part of the Northview shale and into the Pierson limestone in Missouri. Moore (1928) considered the Sedalia to be Osage, but Weller (1948) placed it in the Kinderhook. Branson (1944) placed all but the uppermost part of the Sedalia in the Kinderhook. The top of the Northview is considered by Beveridge and Clark (1952, p. 74) to be the top of the Kinderhook series. Weller (1948) placed the Northview shale in the Kinderhook. The lower Pierson fauna, considered by Spreng (1952) to be Osage, includes the *C. typa typa* faunule.

The *C. typa typa* faunule appears to be present in the Maynes Creek member of the Hampton formation of Iowa that Laudon (1931, p. 426–429) considered to be Kinderhook in age.

The *C. typa typa* faunule occurs in the Andrecito and Alamogordo members of the Lake Valley formation (Laudon and Bowsher, 1941 and 1949) of New Mexico that Laudon and Bowsher (1949, p. 11) considered to be Osage in age.

From these data it would seem that this faunule is both Kinderhook and Osage in age or that it is transitional between Kinderhook and Osage. Either interpretation is a bit naive, since we are actually dealing with a problem in semantics. It appears that some strata characterized by the *C. typa typa* faunule change facies from the type area of the Kinderhook division in Illinois to the type area of the Osage on the Osage River in Missouri. In Illinois these strata occur in the Kinderhook but in Missouri they are, at least in part, in the Osage. The names Kinderhook and Osage were first applied as rock names. In each area this application is justified and necessary, but as time passed the names were given time and time-rock connotations for use elsewhere in the United States. Now we are faced with a dilemma wherein a faunule is in one type area Kinderhook in age but in another type area is Osage in age—purely a semantic problem. Since the names Kinderhook and Osage are tied in their respective type areas to bundles of similar rock strata for mapping purposes there is little hope that this terminology can be adjusted to fit the faunule zonation. As long as the present situation exists, the use of the *C. typa typa* faunule in terms of Kinderhook and Osage age determination across the United States will be ambiguous and misleading. Yet this coral association is one of the more widespread and easily recognized Early Mississippian faunules in North America.

It appears timely that geologists in this country break away from the conventional pattern of utilizing time and time-rock terms based on lithologic subdivisions for regional correlations. The answer seems to be in recognizing faunal zones that can be used in regional correlations; whether faunal zones are also precise time zones is an academic question. Faunal zones are practical. When this practice becomes commonly accepted, I predict that regional "age" correlations for the Mississippian strata will be easier to make.

The system of faunal zonation has been long in use in the Carboniferous of the British Isles. There the lowermost faunal zones are the K zones. The zones, K_1 and K_2, are based on range of *Cleistopora* (Vaughan, 1905). The K zones in Great Britian are succeeded by the Z and C zones, which also were named for the corals that characterize the faunal assemblages.

In North America the lowermost strata of the Mississippian are characterized by the *Cleistopora* faunules described in this paper, although I do not here imply correlation with the British zones. The realistic application of faunal zones in North America will greatly aid in regional correlation and may also help in obtaining a clearer picture of the correlation of the Lower Carboniferous in Europe with the Mississippian of North America.

It is for these reasons that I am not here designating the *C. typa gorbyi* and the *C. typa typa* faunules as Kinderhook or Osage. I wish only to designate them as two faunules of Early Mississippian age, the *C. typa gorbyi* faunule being the older. Faunules underlying the *C. typa gorbyi* faunule and overlying the *C. typa typa* faunule are at present undetermined.

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JOURNAL OF PALEONTOLOGY, V. 35, NO. 5, P. 963–976, PLS. 111–112, 1 TEXT-FIG., SEPTEMBER, 1961

REDESCRIPTION OF *LEIORHYNCHUS QUADRACOSTATUS* (VANUXEM), TYPE SPECIES OF *LEIORHYNCHUS* HALL, 1860 (*RHYNCHONELLACEA*)

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ABSTRACT—The whereabouts of the type or types of *Orthis quadracostata* VANUXEM remains unknown. If they exist, careful search has failed to reveal them. The type locality and horizon are in the vicinity of Cayuga Lake, N. Y., from the Geneseo Shale of Upper Devonian age.

All existing figured hypotypes have been examined and, together with large collections from the type area, form the basis of a full description of the species. *O. quadracostata* is the type species of *Leiorhynchus* HALL.

Citations of the species throughout the world are listed.

INTRODUCTION

THE genus *Leiorhynchus* is one hundred years old.

The genera *Pseudocamarophoria* WEDEKIND, 1926; *Septalaria* LEIDHOLD, 1928; *Zilimia* NALIVKIN, 1937; *Nemesa* SCHMIDT, 1941; *Leiorhynchoidea* CLOUD, 1944; *Calvinaria* STAINBROOK, 1945; *Caryorhynchus* CRICKMAY, 1952; *Sanjuania* AMOS, 1958; and the subgenus *Leiorhynchoides* DOVGAL, 1953, imply, in their definitions, comparisons with the genus *Leiorhynchus*, which is still not clearly circumscribed and, therefore, out of reach of our knowledge and our discussions.

In bringing up the hundredth anniversary of the genus *Leiorhynchus*, the writer's major purpose is to emphasize our extreme indifference towards the type species, *L. quadracostatus* (VANUXEM, 1842), to which the genus is ineluctably bound, and, therby, on our audacity in assigning to it some 150 or so species, subspecies and varieties.

Numerous palliating circumstances exist however. Types remain undiscoverable and may never have existed; in the original publication, the species is scarcely described and represented only by a wood-cut figuring a pedicle valve; the *locus typicus* is not strictly specified and connected with local place names not to be found on maps; the best figures of the species (HALL, 1867, pl. 56, figs. 44–49) which have been reproduced in part (*cf.* synonymy) in subsequent publications, are not faithful and correspond to crushed specimens, partially deformed, which is the common mode of preservation of material in the field. These points have to be straightened out.

Favorable circumstances allowed the author to deal fruitfully with these difficulties. A postdoctorate fellowship granted by the National Research Council of Canada and an Honorary Advanced Fellowship of the Belgian American Educational Foundation enabled the writer to come over from Europe and encounter the understanding and collaboration of highly qualified scientists and institutions. HALL's figured material, kept in the American Museum of Natural History, New York, was put at the writer's disposal by Dr. N. D. NEWELL, who gave him permission to photograph the specimens for publication. All topotypical material in the New York State Museum was made available by Mr. C. F. KILFOYLE as well as a photograph of the only specimen figured by HALL (1867, pl. 56, fig. 48) kept in this institution. Dr. J. W. WELLS of Cornell University provided information concerning the *locus typicus*, helped as a guide in the field, presented the writer with the extremely rare whole and undeformed specimens in his possession and read this paper critically. Much information has been gathered from fruitful discussions with Dr. G. A. COOPER and Dr. D. J. MCLAREN, both of whom made their collections easily accessible. The writer has also a great debt of gratitude towards Dr. C. O. DUNBAR, who introduced him, while a student at Yale University, to the Devonian stratigraphy of New York State.

Search for the holotype or syntypes has

been made by Dr. N. D. NEWELL (Am. Mus. Nat. Hist., N. Y.), Mr. C. F. KILFOYLE (N. Y. St. Mus., Albany), Dr. H. G. RICHARDS (Ac. Nat. Sc. of Philadelphia, Nat. Hist. Mus.), Dr. J. M. WELLER (Univ. of Chicago).

The Geological Survey of Canada provided full laboratory, library, drafting and photographic facilities.

TYPES

The choice of a neotype would not help in the redescription and in our knowledge of *L. quadracostatus*, whose original type or types may still show up somewhere some day.

The following hypotypes have been deposited in the United States National Museum, Washington:

—U.S.N.M. 138768 (pl. 111, figs. 1a–e). Basal 5 feet of Sherburne formation. Lodi Glen (Lodi 7½′ Quadrangle), Seneca County, N. Y. Collectors: J. W. WELLS, D. J. MCLAREN and P. SARTENAER, 1959;
—U.S.N.M. 138769a (pl. 111, figs. 2a–e). Same locality and formation. Collector: J. W. WELLS, 1958;
—U.S.N.M. 138769b (pl. 111, figs. 3a–e). Same locality and formation;
—U.S.N.M. 138769c (pl. 111, figs. 4a–e). Same locality and formation;
—U.S.N.M. 138770 (pl. 111, figs. 5a–b). Top 6 feet of Geneseo formation. Hubbard quarry (Sheldrake 7½′ Quadrangle), Seneca County, N. Y. Collectors: J. W. WELLS, D. J. MCLAREN and P. SARTENAER, 1959;
—U.S.N.M. 138771a (pl. 111, fig. 6). Same locality and formation;
—U.S.N.M. 138771b (pl. 111, fig. 8). Same locality and formation;
—U.S.N.M. 138771c (pl. 111, fig. 9). Same locality and formation;
—U.S.N.M. 138772a,b,c (pl. 112, figs. 5a,b,c). Same locality and formation;
—U.S.N.M. 138773. Same locality and formation.

Hypotypes 138769a and 138769b have been photographed and plaster casts have been taken before grinding (*see* serial sections in text-fig. 1, B and A); casts as well as the remainder of the specimens are deposited in the U.S.N.M. The remainder of hypotype 138773 is also accompanied by a cast taken before grinding (*see* serial sections in text-fig. 1, C).

One hypotype is in the Paleontological Collection (no. 40605) of the Department of Geology, Cornell University, Ithaca, N. Y. It derives from the same locality and formation as hypotypes 138768, 138769a,b,c; its locality number is 111s.

The two specimens represented on plate 111, figure 7 are part of HALL's collection at the Am. Mus. Nat. Hist., N. Y.

The remainder of the material is partly at the Geological Survey of Canada, Ottawa (G.S.C. loc. 41325) and partly at the *Institut royal des Sciences naturelles de Belgique*, Brussels (I.G. 22046).

TYPE LOCALITY

The information given in VANUXEM's original paper on the location of his new species found in the "Genesee Slate" is: "The fossils of the wood-cut[1] were not generally diffused, but quite numerous in a few localities on Cayuga lake; and the best localities for obtaining them are the ravines near Ogden's ferry, towards the upper part of the mass."

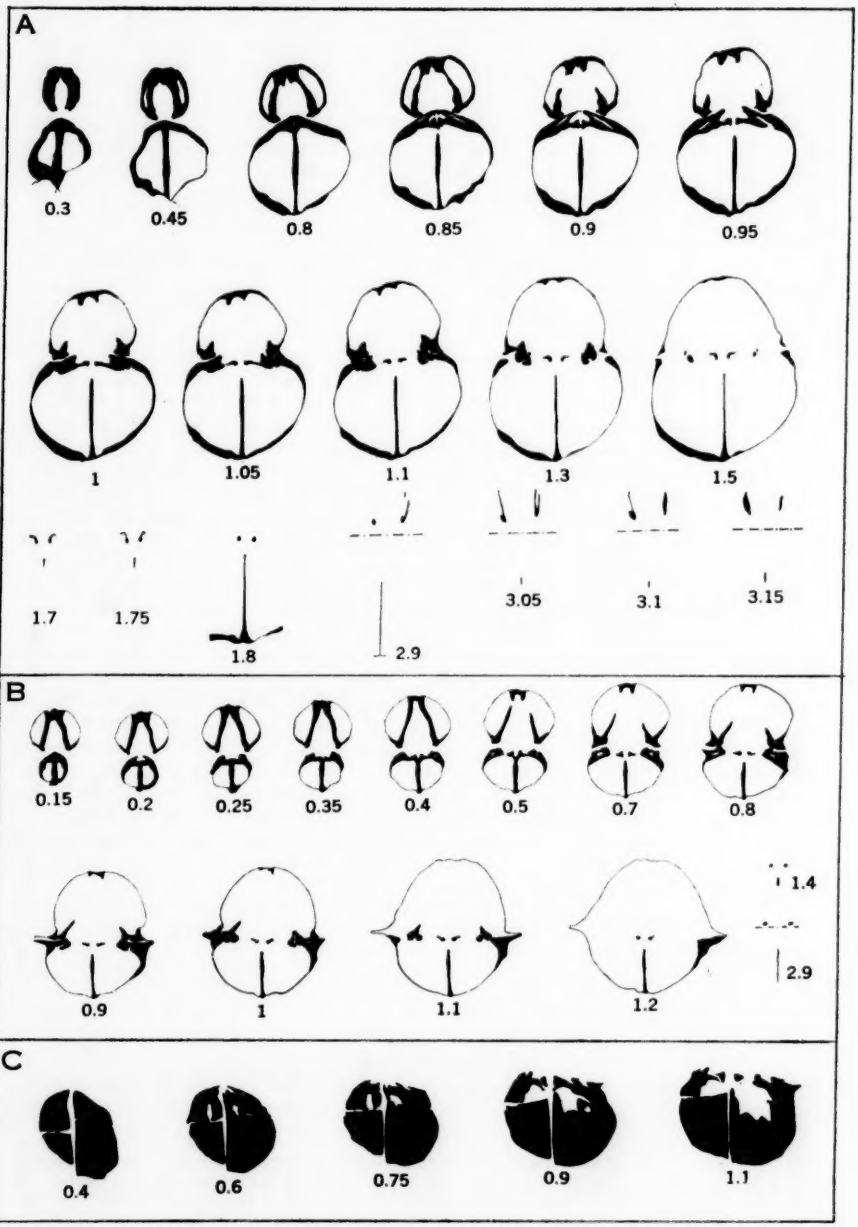
Kidders and Kings Ferry Station are local names called after families who operated the ferry. They lie on the west and east shore of Cayuga Lake respectively, a short distance south of Sheldrake (Sheldrake Quadrangle, 7½ minute series, New York). The Ogden of VANUXEM's description was the family name of another operator of the same ferry. The last boat used to join the shores of Cayuga Lake was the "Busy Bee"; she was abandoned in 1912, on the west shore at Kidders, where she sank and is still partly visible.

There is no definite indication whether VANUXEM had the eastern or the western end of the ferry in mind; most probably, it was the eastern end once known as Port Ogden. However, this point is of minor importance, as the same beds appear in the ravines on either side of the lake. The Devonian strata here dip to the south with only a slight western component. It is more appropriate in this case to speak of a type area than of a type locality.

TYPE HORIZON

Referring to the "Genesee slate" in parts of a few towns, VANUXEM (1842, p. 169)

[1] These fossils are, under their present names: *Orbiculoidea lodensis, Leiorhynchus quadracostatus, Barroisella spatulata, Schizobolus truncatus.*



TEXT-FIG. 1—*Leiorhynchus quadracostatus* (VANUXEM), serial sections, *A*, figures are the distance in mm. of the section forward of the ventral umbo, sections show the reduced "septalium," hypotype USNM 138769b, ×3½; *B*, figures are the distance in mm. of the section forward of the ventral umbo, hypotype USNM 138769a, ×3½; *C*, figures are the distance in mm. of the section forward of the crest of the dorsal umbo, one of the very rare almost uncrushed and best preserved brachial valve in a septarian concretion from the *stratum typicum*, in spite of the numerous cracks the main structures may be observed and compared with those in the figures above, in the last section the septum is artificially contoured in order to distinguish it from the secondary calcite around, dimensions of the specimen: l.: 1.95(?), w.: 2.11(?), hypotype USNM 138773, ×3½.

states that it "may readily be found by its black color, slaty fracture, and being between the Tully limestone and the sandstone flags of the base of the Ithaca group." This observation has a general application within the limits of the type area. In present terminology, the *stratum typicum* is the Geneseo black shale between the Tully limestone below and the Sherburne flagstone above.

In the Geneseo shale, *L. quadracostatus* has only been found in the upper eight feet. There can be no doubt that it is VANUXEM's species, for there is no other rhynchonellid associated with it or in the Geneseo shale. Also, there is no danger the species might have been overlooked on account of its rareness as VANUXEM writes (1842, p. 168) that the species is "quite numerous in a few localities on Cayuga lake." One has to go down to the Windom member of the Moscow formation or up to the middle part of the Ithaca formation, to find other species attributed to the same genus; this does not include forms at the base of the Sherburne which are considered as conspecific by the writer.

Thus, the type horizon is very restricted.

The upper 8–10 feet of the Geneseo shale are the lowest strata in central New York in which manticoceratid goniatites (*Ponticeras perlatum*) have been found; their age is Upper Devonian. This horizon is believed to be just above the Middle-Upper Devonian boundary, but the problem of this limit cannot be considered as solved.

CONDITIONS OF OUTCROP

Where it occurs in abundance, *L. quadracostatus* is concentrated in lenses in the black shale; specimens are crushed, deformed and mostly decalcified. *Barroisella spatulata* and *Schizobolus truncatus* are also abundant species and, although they occur sometimes with *L. quadracostatus*, there are many lenses in which the last-named species occurs to the exclusion of all others. *Orbiculoidea lodensis* is less abundant. The following species are rather rare: *Ponticeras perlatum*, *Tornoceras peracutum*, *Pterochaenia fragilis*. Some fish and some plant fragments are also found from time to time as well as few very rare other species. This faunal (and floral) association is well shown in the Hubbard quarry a little more than two miles south of Sheldrake, east of Route 89 and just south of Lively Run. Most of the collecting was done here because of exceptional—and probably temporary—favorable conditions: a fresh excavation in the top beds of the Geneseo shale, from the base of the Sherburne flagstone down. Another reason for extensive collecting in the Hubbard quarry is that in most of the places in the region, where the upper Geneseo and the lower Sherburne can be seen in contact, the

EXPLANATION OF PLATE 111

FIGS. *1–9*—*Leiorhynchus quadracostatus* (VANUXEM), *1*a-e, ventral, dorsal, frontal, apical and lateral views; the only satisfactorily preserved juvenile specimen; median plications: $\frac{3}{2}$; hypotype USNM 138768, ×1; *2*a–e, ventral, dorsal, frontal, apical and lateral views; number of plications: median ($\frac{4}{4}$), lateral (4 or 5), hypotype USNM 138769a, ×1; *3*a–e, ventral, dorsal, frontal, apical and lateral views, fine radial "striation" visible, number of plications: median ($\frac{5}{5}$), lateral (4), hypotype USNM 138769b, ×1; *4*a–e, ventral, dorsal, frontal, apical and lateral views, number of median plications: $\frac{4}{4}$, hypotype USNM 138769c, ×1; *5*a–b, lateral and apical views, one of the rare uncrushed specimens from the *stratum typicum* showing the shape of the species, hypotype USNM 138770, ×1; *6*, large pedicle valve showing the muscular scars and the ovarian impressions, number of median plications: 4, hypotype USNM 138771a, ×1; *7*, two pedicle valves from HALL's collection at the Am. Mus. Nat. Hist., N. Y., 3 median plications on both valves, ×1; *8*, brachial valve showing ovarian impressions, hypotype USNM 138771b, ×1; *9*, large pedicle valve, 5 median plications and at least 8 lateral plications, on each side one lateral plication is divided, hypotype USNM 138771c, ×1.

1a

1b

1c

1d

1e

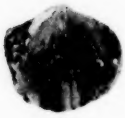
2a

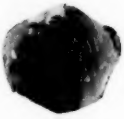
2b

2c

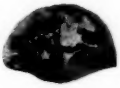
2d

2e

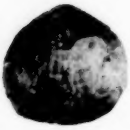

3a

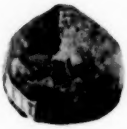

3b

3c


3d

3e


4a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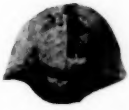
4c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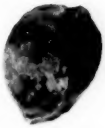
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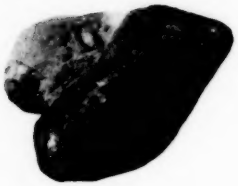
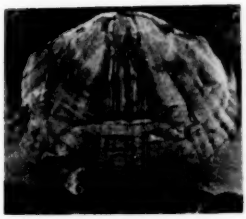

5a

5b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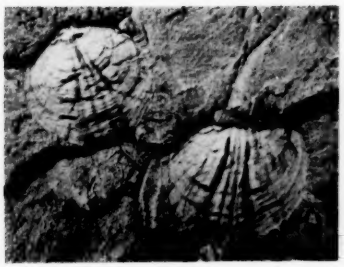

7

8

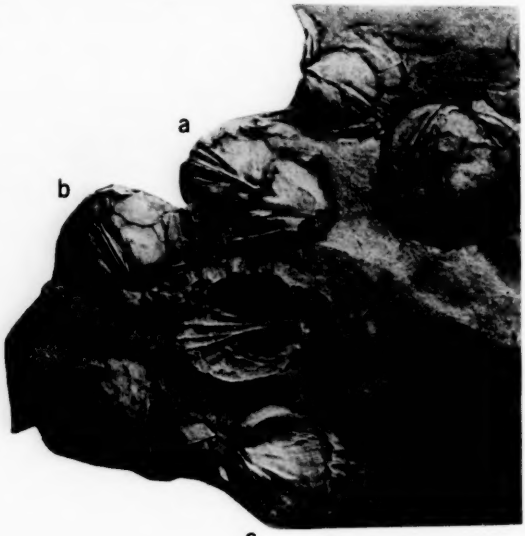
9

1

2

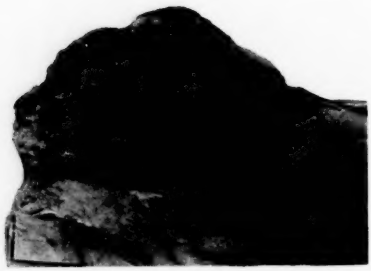
3

4



5

6



7

outcrop is almost inaccessible and collecting very difficult; this has been pointed out by WELLS (1959, p. 30).

Septarian concretions are abundant in the *Leiorhynchus* bearing beds; they are flattened and vary from 4–6 inches in length and width (sometimes in diameter) and 4 inches in height, to exceptional sizes of 16 inches in length or width and 6 inches in height; they may be elongated. The best preserved *L. quadracostatus* are found occasionally in these concretions and only from these specimens may the shape of the species be deduced.

STRATIGRAPHIC EXTENSION OF THE SPECIES IN THE TYPE AREA

L. quadracostatus has been found only in the upper eight feet of the Geneseo. Outside the *stratum typicum*, a few specimens belonging, according to the writer, to the same species, have been collected in the lower five feet of the Sherburne flagstone, from calcareous lenses. This means that the species is known in a thickness of rocks of only thirteen feet.

MATERIAL

Approximately 2000 specimens, almost exclusively from Hubbard quarry. The remainder were collected in Lodi Glen.

Specimens from other localities have been studied in the collections from the Am. Mus. Nat. Hist., N. Y., including most of HALL's hypotypes, from the New York State Museum, Albany, including one of HALL's hypotypes, from the Department of Geology, Cornell University, Ithaca, and from the Peabody Museum, Yale University, New Haven.

SYNONYMY[2]

Four ribbed orthis (*O. quadracostata*) VANUXEM, 1842, p. 168, fig. 42, no. 2, *in textu*.

Atrypa (*Orthis*) *quadricostata* HALL, 1843, p. 223, fig. 95, no. 2, *in textu* (=fig. 42, no. 2, *in textu*, *in* VANUXEM, 1842).

Atrypa quadricostata HALL, 1843, p. 223, tables of organic remains, no. 51, fig. 7 (=fig. 2 *a dextra*) (=fig. 42, no. 2, *in textu*, *in* VANUXEM, 1842).

Leiorhynchus quadricosta HALL, 1860, p. 75.

Leiorhynchus quadricostata HALL, 1860, p. 86. HALL, 1867, p. 357–358, pl. 56, figs. 44–49.

Leiorhynchus quadricostatum MILLER, 1889, p. 347, fig. 569 *in textu* (=fig. 42, no. 2, *in textu*, *in* VANUXEM, 1842). GRABAU, 1899, p. 233, fig. 143, *in textu* (=figs. 47,48,49 *in* HALL, 1867). SHIMER and GRABAU, 1909, fig. 357d *in textu*, p. 289 (=fig. 49 *in* HALL, 1867).

Rhynchonella (*Orthis*, *Atrypa*) *quadricostata* LESLEY, 1892, p. 1325, fig. *in* pl. CLXXI, p. 1326 (=fig. 42, no. 2, *in textu*, *in* VANUXEM, 1842).

Liorhynchus quadricostatus HALL and CLARKE, 1894a, pl. LIX, fig. 21 (=fig. 49 *in* HALL, 1867), fig. 22 (=fig. 45 *in* HALL, 1867). HALL and CLARKE, 1894b, p. 827, pl. 43, fig. 22 (=fig. 49 *in* HALL, 1867).

DESCRIPTION

External characters.—The shell is inflated, inequivalve, globulose and generally of medium size, but large sizes can be reached (pl. 111, figs. 6,9; pl. 112, fig. 7).

[2] Restricted to the type area. See further comments under the paragraph "discussion of synonymy and geographic distribution."

EXPLANATION OF PLATE 112

FIGS. *1–7*—*Leiorhynchus quadracostatus* (VANUXEM), *1*, brachial valve figured by HALL (1867, pl. 56, fig. 45), median plications: 4, plication on the left is lateral, locality: Big Stream Point, Seneca County, N. Y., AMNH ,×1; *2*, brachial valve figured by HALL (1867, pl. 56, fig. 48), number of plications: median (4), lateral (10), locality: Lodi, Seneca Lake, N. Y., NYSM, Albany, ×1; *3*, brachial valve figured by HALL (1867, pl. 56, fig. 44), median plications: 4, locality: Big Stream Point, Seneca County, N. Y., AMNH, ×1; *4*, brachial valve figured by HALL (1867, pl. 56, fig. 46), number of plications: median (4), lateral (8 or 9), locality: Big Stream Point, Seneca County, N. Y., AMNH, ×1; *5a–c*, specimens showing internal structures and muscle scars, *5a* shows fine radial "striation," hypotypes USNM 138772a,b,c, ×1; *6*, brachial valve figured by HALL (1867, pl. 56, fig. 47), median plications: 6, locality: East shore, Cayuga Lake, N. Y., AMNH, ×1; *7*, large pedicle valve figured by HALL (1867, pl. 56, fig. 49), number of plications: median (5), lateral (7), fine radial "striation" visible, locality: East shore, Cayuga Lake, N. Y., AMNH, ×1.

Umbonal regions are both tangent to a plane perpendicular to the plane of commissure; the dorsal umbonal region may stand a little more posteriorly than the ventral. The greatest length of the shell is measured between this vertical plane and the frontal commissure at the summit of the tongue. The greatest thickness of the brachial valve lies around mid-length, that of the pedicle valve from posterior $\frac{1}{3}$ to $\frac{4}{10}$ of the length. The longitudinal curvature of the brachial valve is almost symmetrical on each side of the mid-length point. The greatest width is at or slightly forward of mid-length.

In cardinal view, the contour of the brachial valve is helmet shaped. Ventral and dorsal views show a rounded to elliptical contour; the ventral view may have a subpentagonal aspect.

Sinus and fold are weakly developed; thus, the median longitudinal curvature is similar to that of the flanks, while median transversal sections show uninterrupted curves. Slopes of the brachial valve drop with increasing abruptness to the commissures. Ventral flanks, in contrast, have decreasing slopes starting from a median protuberance including a larger area than just the umbonal region.

The sinus starts at a distance from the beak varying between $\frac{45}{100}$ to $\frac{58}{100}$ of the length of the shell (or between $\frac{55}{100}$ to $\frac{60}{100}$ of the unrolled length of the pedicle valve). Sinus and fold start with a width equal to about half their width at the front. The sinus passes imperceptibly to the flanks; its width, estimated between the junctions of lateral and frontal commissures, varies between $\frac{55}{100}$ and $\frac{65}{100}$ of the width of the shell. Depth of sinus is only one to two times, rarely more, the height of the low median plications. The bottom of the sinus is flat or slightly convex.

The tongue is never recurved posteriorly and its top corresponds to the most anterior part of the shell at the frontal margin; this top lies between $\frac{1}{4}$ to $\frac{4}{10}$ of the height of the shell below the summit.

The low fold starts at a distance from the beak varying from $\frac{30}{100}$ to $\frac{45}{100}$ of the length of the shell (or from $\frac{40}{100}$ to $\frac{45}{100}$ of the unrolled length of the brachial valve). The fold is gently curved and sometimes flat.

At the commissures, which are sharp, valves join at an angle close to 90°, but at the cardinal commissure and posterolaterally, valves are convexo-concave and join at a smaller angle. Sometimes, this reversal in curvature is very pronounced. The frontal commissure is incised by the plications, the lateral commissures little or not at all. Lateral commissures are located rather high, as both valves are inflated.

The ventral beak is slightly incurved and does not overhang the hinge line. It is however, in contact or nearly in contact with the inflated brachial umbo. Because of this condition and the scarcity of well preserved specimens, little can be said about the foramen, delthyrium and deltidial plates. In one specimen (hypotype U.S.N.M. 138769c), there seems to be a small rounded foramen resulting from resorption of the beak. The interarea is, in the two best preserved specimens, $\frac{69}{100}$ and $\frac{79}{100}$ times the width of the shell. It is limited by well-marked ridges near the beak which become less distinct towards the flanks of the valve.

Ornamentation.—About 95% of the crushed specimens show only the brachial valve; ecological or taphonomical factors, or both, must account for this situation.

On the 214 brachial valves on which median plications have been studied, 11 specimens (5.10%) had 6, 21 (9.80%) had 5, 166 (77.60%) had 4 and 16 (7.5%) had 3. Hence VANUXEM'S name: *quadracostata*. In specimens with 6 plications, 3 start from the beak and divide anteriorly at about one third of the shell length forward (pl. 112, fig. 6, right). When there are 5 plications, commonly 3 extend from the beak and 2 divide, or 4 may start at the beak and one divides. With 4 plications, in most (83%) cases, 3 start from the beak and the median divides (pl. 112, figs. 2,3) at a variable distance (usually between the $\frac{1}{3}$ and $\frac{2}{3}$ of the length) forward of the beak; in the remainder (17%), no division has been observed. When there are 3 plications, all 3 start from the beak, except in one specimen.

In the 23 pedicle valves which show median plications, 4 specimens had 5, one had 4 and 18 had 3. In none of the specimens with 3 plications has a division been observed and plications start from the beak. The specimen with 4 plications is poorly preserved. Of the specimens with 5 plica-

tions, 3 have a single division and the remaining specimen two. Plate 112, fig. 7, shows a specimen with 5 plications, none of them being divided unless such a division should take place very near to the beak, where it would be unobservable.

Median plications in both valves are of low relief, but not obsolescent, rounded to flatly rounded and of variable and sometimes great width (varitaions can be seen in the plates); this inequality in width of the plications is chiefly, although not always, due to the divisions.

Median furrows are seldom equal in width to the plications; commonly, they vary between $\frac{1}{2}$ and $\frac{1}{4}$ the width of the plications.

Lateral plications are seldom seen owing to poor preservation, thinness of the shell and their general obsolescence. One (pl. 112, fig. 1, left side) to 10 (pl. 112, fig. 2) lateral plications have been observed. Lateral plications extend from the umbonal region. Lateral plications are flatly rounded, decreasing in width from the sinus and fold towards the margins; they are simple, but in one specimen, one plication is divided on each flank (pl. 111, fig. 9).

Very seldom, a radial "striation" can be observed (pl. 111, figs. 3a,b,c,e; pl. 112, figs. 5a,7). The significance of this "striation" is not clear.

Growth lines are common.

Dimensions.—Here are the dimensions (in cm.) of the 4 best specimens (specimens of columns 1, 3, 4, are represented on plate 111):

The above specimens were collected from the basal 5 feet of the Sherburne flagstone. Specimens from the Geneseo shale are usually bigger and may reach sometimes large dimensions; the greatest length and greatest width which have been measured are, respectively: 3.80 cm. and 4.30 cm.

Internal characters.—Shell is thin, but thicker in the apical region.

Dental plates are separated from the walls of the shell by well developed umbonal cavities. They are short: less than $\frac{1}{10}$ of the length of the shell or about $\frac{1}{5}$ of the unrolled length of the pedicle valve. They are stout and slightly concave anteriorly.

Teeth are small, short and robust.

The septum is stout, with diminishing height anteriorly. The length of the septum can be as much as $\frac{1}{2}$ of the length of the shell, or $\frac{3}{4}$ of the unrolled length of the brachial valve. Posteriorly (pl. 112, fig. 5, text-fig. 1), the septum is thickened lensewise; anteriorly, it separates the adductor scars and functions as an *euseptoidum*. Many crushed specimens split along the middle of the septum (pl. 112, figs. 3,5, text-fig. 1C).

The septum supports a short "septalium" or "crural trough." The "septalium" supports a divided hinge plate. The septum ceases to support the "septalium" when the level of articulation is reached or even before.

Crura reach as far as $\frac{1}{5}$ of the length of the shell. They extend anteriorly from the dorso-anterior margin of the hinge plate (text-fig. 1A,B) and become filiform and end

	U.S.N.M. 138769c	Cornell Univ. no. 40605	U.S.N.M. 138769b	U.S.N.M. 138769a
length (l.)	1.85	1.77	1.65(?)	1.60
width (w.)	1.96	1.92	1.87(?)	1.87
l. pedicle valve (p. v.) unrolled	2.55	2.45	2.15(?)	2.20
thickness (t.)	1.57	1.27	1.26	1.04
t.p.v.	0.57	0.57	0.44	0.46
t.b.v.	1	0.70	0.82	0.58
l./w.	0.94	0.92	0.88(?)	0.86
t./w.	0.80	0.66	0.67(?)	0.56
t./l.	0.85	0.72	0.76(?)	0.65
shoulder angle[3]	117°	120°	120°	125°

[3] The shoulder angle is the one measured at the beak of the pedicle valve in ventral view, the plane of commissure being horizontal. Although it might be sometimes equivalent to the apical angle, it is not usually.

trough-shaped distally; they curve gently ventrally in the same fashion as the cardinal commissure, but their trough-shaped section is strongly recurved.

The dorsal muscle scars are spindle shaped (pl. 111, fig. 8; pl. 112, figs. 5,6), but is has been so far impossible to recognize the two pairs of adductor scars; most likely, as suggested by figure 5b, plate 112, one pair is smaller than the other and formed by the two tear-like impressions located at the posterior end of the elongated pair.

Ventral muscle scars are very poorly preserved, if at all; the best preserved are represented on plate 111, figure 6 and plate 112, figure 5c.

Ovarian impressions are distinctly marked.

Serial sections show how variable some structures can be depending on the orientation of the plane of grinding; this being chosen, as a rule, perpendicular to the plane of commissure, height of the shell is an important factor.

Growth.—The only whole juvenile specimen (pl. 111, figs. 1a–e) in satisfactory state of preservation, is from the Sherburne formation, and has the following dimensions (in cm.):

	l.	w.	l.p.v. unrolled	t.	t.p.v.	t.b.v.	l./w.	t./w.	t./l.	shoulder angle
U.S.N.M. 138768	1.23	1.31(?)	1.60	0.78	0.33	0.45	0.94(?)	0.60(?)	0.63	105°

More material is available for estimating juvenile characters.

The species has a non constant and monocyclic curvature growth (SCHMIDT, 1937). Ratios t./w. and t./l. show that, in juvenile stages, length and width are proportionately the most developed dimensions; thickness increases noticeably in later stages when width and length increase relatively little. Columns 2 and 4 of the table of dimensions given under the general description show intermediate stages.

In consequence, a low thickness ratio is associated with other juvenile characters: brachial valve not inflated; dorsal umbonal region not projected posteriorly; dorsal flank gently curved; ventral beak more prominent; valves joining under smaller angles at the frontal commissure and at the anterior parts of the lateral commissures.

Sinus and fold are mere undulations with ill-defined limits.

DISCUSSION OF SYNONYMY AND GEOGRAPHIC DISTRIBUTION

As the object of this paper is the redescription of the type species of *Leiorhynchus*, the synonymy refers only to specimens and collections, which are, without doubt, derived from the same area and the same stratigraphic level as the original material.

Specimens reported as this species from other areas and horizons have yet to be examined critically, definitely to establish their real affinities with or differences from *L. quadracostatus*. In that respect, the problem is still exactly as CHADWICK (1935, p. 305–306) saw it. In order to clear the way, the horizon and locality of reported occurrences of the species from other than the type area are mentioned under the following headings: (1) New York State; (2) U. S. A. (outside N. Y.); (3) outside the U. S. A.

New York.—WILLIAMS (1882, p. 187–188) in the Genesee slate, the Ithaca shale and, as "an imperfect specimen of the *quadracostatus* type", in the Marcellus of central N. Y. State; WILLIAMS (1884, p. 9,14) in the Genesee shale of Burdick's Glen (now, Esty's Glen, 2,5 mi. from S–E corner of Cayuga Lake) and, as "specimens (of *Leiorhynchus*) presenting more or less fully the distinctive characters of *L. limitaris*, of *L. quadricostata*, or of *L. mesocostalis*," in an intrusion of Ithaca fauna in the Portage group fauna; CLARKE (1885a, p. 24,33,70), in the Genesee shales in Ontario County; CLARKE (1885b, p. 18,19), in shales below and above the *Styliola* layer and in Genesee shales in Ontario County; CLARKE (1889, p. 61 (or p. 407)), in the bituminous shales of the Marcellus epoch and "continuing its

existence into the late faunas of the Hamilton group"; CLARKE (1891a, p. 88,89; 1891b, p. 162), in the Genesee shales of the Canandaigua Lake region; CLARKE (1897 and 1898, p. 58,80), as a "*Liorhynchus*, which at maturity is of large size and has the aspect of *L. quadricostatus*", just below the Portage sandstones, in Naples, and in the Genesee slate in Plum creek, Yates County; CLARKE (1899a, p. 93–94,111), in Wiscoy creek and at Java; CLARKE (1899b, p. 40), as "a large shell, having at maturity the aspect of *L. quadricostatus*, but with well developed lateral plications", in the Naples fauna just below the Portage sandstones in the Naples section; LUTHER (1902, p. 622), at 600' above the Genesee shales in Grimes gully; CLARKE and LUTHER (1904, p. 49, p. 58), in the Canandaigua shales proper (Hamilton beds) and the Genesee shale of Canandaigua and Naples quadrangles; CLARKE and LUTHER (1905, p. 4), in the Genesee shale of Watkins and Elmira quadrangles; CLARKE (1905, p. 64), as "*Liorhynchus quadricostatus ?*", in the Ithaca beds at St. Mary's falls; LUTHER (1906, p. 41,49), in the Genesee black shale of Penn Yan and Hammondsport quandrangles and in the Grimes sandstone in the western part of the Penn Yan quadrangle (or at Naples); CLARKE and LUTHER (1908, p. 50), towards the top of the black Genesee shale at Mount Morris; LUTHER (1909, p.20,26,28,30), in the Ludlowville shale, Genesee shale, West River shale of the Geneva and Ovid quadrangles, and in the sandstone of the Cashaqua shale, at Ovid; KINDLE, TARR and WILLIAMS (1909, p. 6–7), in the Genesee shale of the northeastern corner of Watkins Glen quadrangle; LUTHER (1910, p. 26,27, 28), in the Genesee black shale and the West River dark shale of the Auburn and Genoa quadrangles, and in the Genundewa limestone in Salmon creek; LUTHER (1911, p. 16), in the Genesee black shale of Honeoye and Wayland quadrangles; GOLDRING (1931, p. 397), in the Genesee beds; von ENGELN (1932, p. 48), in the Genesee shale of the Finger Lakes area; CHADWICK (1935, p. 313, 317), in the Genesee and Naples group[4]; GROSSMAN (1944, p. 57), in the Genesee group.

[4] This might include specimens from Pennsylvania and even Ohio.

U. S. A. (outside New York State).—

Arkansas

WILLIAMS (1895, p. 94,98), in the Spring Creek limestone, at Spring Creek; WILLIAMS (1900, p. 343,345–346,353), in the same limestone; GIRTY (1905, p. 12), as a "*Leiorhynchus* like *L. quadricostatum*", in the same limestone and in the Fayetteville shale. The Arkansas form has been put by GIRTY (1909, p. 27) under *Liorhynchus* aff. *mesicostale* and, in 1911 (p. 54,58–59), under his new species: *L. carboniferum* of the Moorefield shale.

Indiana

WHITFIELD (1875, p. 179–182), in the Black Slate of Lexington, Scott County; BORDEN (1876, p. 171), in the New Albany black shale, a short distance northwest of North Vernon, Jennings County; NETTELROTH (1889, p. 71–72), in the Genesee shales and in the rotten hornstone just below, at the Falls of the Ohio and at Lexington; KINDLE (1899, p. 18,24–25,61,111), including existing literature and collections, cites the species in the New Albany shale in Scott County (Lexington section) and Jennings County, in the Sellersburg beds at the Ohio Falls section, in the Jefferson limestone in Harrison County and at New Albany, and, perhaps, in the Rockford limestone at Crothersville; KINDLE (1901, p. 544, 571, pl. 1, figs. 5,5a), in the New Albany shale, 3 or 4 feet above the Sellersburg beds, ¾ of a mile east of Lexington and in the New Albany shale at Helt's Mill, Jennings County; CAMPBELL (1946, p. 841,842,845), in the Blocher formation (in the lower bed A1), at many localities not given but one at 1½ mile east of Hayden.

Kentucky

NETTELROTH (1889, p. 71–72), in the Genesee shales and in the rotten hornstone just below at the Falls of the Ohio; GIRTY (1898, p. 384,386,391, fig. 5, p. 395), at the base of the Devonian black shale supposed to be of Genesee age, near Jeffersonville, Montgomery County and near Indian Fields, Clark County; KINDLE (1899, p. 28, 61,111), perhaps in the New Albany at Brooks; KINDLE (1901, p. 540), in the Sellersburg beds in the Ohio Falls section;

KINDLE (*in* KINDLE and WILLIAMS) (1905, p. 19,20), in the Sellersburg cement beds at Louisville and, as *Leiorhynchus* cf. *quadricostatum*, near Brooks in Bullitt County; SAVAGE (1930, p. 17,65,78–79,134–135), in the lower layers of the New Albany shale near Irvine, Estill County, at Pott's Store, Casey County and near New Hope, Nelson County.

Nevada

HALL and WHITFIELD *in* KING (1876, p. 479), in black shales on top of the Chemung, White Pine Mountains; MEEK (1877, p. 79–80, pl. III, figs. 9,9a–b), as "*Leiorhynchus quadricostatus* ?", and HALL and WHITFIELD (1877, p. 200–201), in the same black shales at the same locality; WALCOTT (1884, p. 5), in the same black shale (White Pine shale) in the same district; GIRTY (1905, p. 11–12), as "a *Leiorhynchus* resembling *L. quadricostatum*", in the same shale and district.

The Nevada form has been put by GIRTY (1909, p. 27) under *Liorhynchus* aff. *mesicostale*, and, in 1911 (p. 54,58–59), in his new species: *L. carboniferum*.

Ohio

NEWBERRY (1873, p. 154), in the Huron shale.

Oklahoma

GIRTY (1905, p. 12), as "a *Leiorhynchus* like *L. quadricostatum*", at the base of the Caney shale.

The Oklahoma form has been put by GIRTY (1909, p. 26–27) under *Liorhynchus* aff. *mesicostale* and, in 1911 (p. 54), under his new species: *L. carboniferum*.

Pennsylvania

STEVENSON (1882, p. 80,230), in the Chemung of Bedford County; LESLEY (1889, p. 307), in the Salina shale, in E. W. CLAYPOLE'S collection, at Cedar run, Perry County; WILLARD (1935, p. 1201), as *Liorhynchus* cf. *quadricostatum*, in the Portage group; WILLARD and CLEAVES (1938, p. 16), as *Liorhynchus* cf. *quadricostatum*, in the Trimmers Rock sandstone; WILLARD (1939, p. 212, pl. 19, fig. 33), as *Liorhynchus* cf. *quadricostatum*, in the Ithaca facies of the Trimmers Rock fauna.

U. S. S. R.—In the last decade, the New York species, and its variety *kamense*, has been mentioned commonly, and sometimes figured, in the Russian literature,[5] i.e.: KRYLOVA (1951, p. 118–120, pl. II, fig. 8); DOMRATCHEV (1952, p. 63,64,66); TIKHII (1953, p. 129); FEDOROVA (1955, p. 10,22, pl. II, fig. 3); KOURBANOV *in* ELLERN, IVANOV and KOURBANOV (1955, p. 112, 123–124, pl. II, fig. 4); MIKRIOUKOV (1955, p. 215); PETRENEVA (1955, p. 266, 270–271); BATANOVA (1957, p. 136); FILIPPOVA, LIACHENKO, ARONOVA, GASSANOVA, MAIZEL and SOKOLOVA (1958, p. 94,96,97,98,103,104, 105); MARKOVSKII (1958, p. 253); LIACHENKO (1959, p. 64,65,66,67,68,70,152–153,230–231); etc . . .

In the U. S. S. R., the species and its variety have been collected from the Domanik beds (Lower or Middle Frasnian depending on the author; Middle Frasnian seems to encounter general agreement now) and the *Gephyroceras* zone, the Semilouki beds (Middle Frasnian, middle part) and the Roudkino horizon (Middle Frasnian, lower part).

The geographical distribution for the species is: central and eastern part of the Russian platform, Kara-Taou range, Oural Mountains (occidental slope mostly), Volga region and between Oural Mountains and Volga. The variety has only been cited from the northwestern part of the A. S. S. R. of the Tatars and the central part of the Russian platform.

NOTES ON NOMENCLATURE

The species was introduced by its founder under the name *Orthis quadracostata*. This original spelling should be preserved as there is no evidence of an error of transcription, nor of a *lapsus calami*, nor of a typographical error (Art. 19 of the "Règles"). Only the ending of the species name will be different should the gender of the genus change; therefore, *Leiorhynchus quadracostatus* is the only correct spelling.

In 1860, HALL considered *Atrypa quadricosta* and *A. mesacostalis* as "types of the genus". Not until 1887 was *L. quadracostatus* chosen as the type species by OEHLERT (p. 1308); it is therefore a genolectotype.

[5] The French phonetic system has been consistently used for transcription of Russian names.

In spite of the fact that HALL's original description makes it highly probable that the Greek word *leios* was used in the construction of *Leiorhynchus*, HALL did not say so. Even if subsequent etymologies given by OEHLERT (1887, p. 1308), MILLER (1889, p. 347), NETTELROTH (1889, p. 71), GRABAU (1899, p. 232) confirm this probability, the basic fact is not altered. This led the writer (1959) to discuss and reject the introduction of the genus *Nudirostra* COOPER and MUIRWOOD, 1951, which is a junior synonym of *Leiorhynchus*.

The genus *Liorhynchus* HALL, 1893,[6] being preoccupied by the genus *Liorhynchus* RUDOLPHI, 1801, has to be rejected; it is an objective homonym. It is also a junior synonym of the genus *Leiorhynchus* HALL, 1860, even if it has been proposed by the founder of this last genus (HALL, 1893, p. 193).

CONCLUSIONS

The absence of any types for *L. quadracostatus*, the defective information on which the species was founded and the poor state of preservation in the field have led to complications. As the species is the type species of a long established genus, the need for clarification appeared so pressing that the writer (1955) started to investigate the matter on the slender evidence to be found in the literature and from an examination of those of HALL's (1867) figured hypotypes kept in the Am. Mus. Nat. Hist., N. Y. The present paper must necessarily have the effect of restricting the usage of the genus *Leiorhynchus* to forms related to the type species as now described. Hence, some of the statements made in 1955 have to be rejected or restricted in the light of the following conclusions:

1.—The genus *Leiorhynchus* is more restricted than has hitherto been considered. Many species attributed to it will have to be assigned to other genera and subgenera, known or new:

2.—Species and varieties which remain in the genus *Leiorhynchus* include: *castaneus* MEEK; *globuliformis* var. *chagrinanus* PROSSER; *nevadensis* WALCOTT; *pavlovi* NALIVKIN and its varieties *kasanensis* ELLERN and IVANOV, *markovskii* LIACHENKO and *serdobensis* LIACHENKO; *quadracostatus* var. *kamensis* KOURBANOV; *taimyricus* NALIVKIN;[7]

3.—Species and varieties doubtfully assigned to the genus *Leiorhynchus* include: *carya* CRICKMAY; *inelegans* MCLAREN; *tumidus* KAYSER and its varieties *quadricostatus* MAILLIEUX and *tricostatus* MAILLIEUX. The writer is still concerned with the generic significance—or the significance at all—of the absence or coalescence of dental plates. If this structural characteristic should prove of generic—or of subgeneric value, as the writer is inclined to believe—*Caryorhynchus* CRICKMAY would be available. MCLAREN (personal communication and in press) considers *Caryorhynchus* as very probably a synonym of the genus *Leiorhynchus;*

4.—Specimens of the following species and variety may belong to the genus *Leiorhynchus*, but whose interiors are unknown: *Gypidula mansuyi* GRABAU; *Leiorhynchus deprati* var. *obesus* GRABAU;

5.—Species belonging to a closely related genus or a subgenus of *Leiorhynchus* include: *huronense* NICHOLSON, *kelloggi* HALL, *laura* BILLINGS, *multicostum* HALL, etc . . . Not enough is known presently about *globuliformis* VANUXEM, to decide if it belongs to this group or not;

6.—The genus *Calvinaria*, which has been put by the writer (1955) into the synonymy of *Leiorhynchus*, on the base of insufficient information on *L. quadracostatus*, is a valid genus. MCLAREN, in a paper in press, will give the differences between the two genera.

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[6] On account of the question mark put by OEHLERT (1887, p. 1308) in front of *Liorhynchus*, the genus cannot be attributed to him without question.

[7] The validity of the species cited in the conclusions is not considered here.

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PERFOROSPORITES, A NEW GENUS OF PLANT SPORES FROM THE LOWER DEVONIAN OF EASTERN CANADA

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ABSTRACT—A new genus of plant spores, *Perforosporites*, is described from Lower Devonian strata of Gaspé, Quebec. The genus is monotypic, and is characterized by pores in a thick spore wall. Present evidence suggests its restriction to Lower Devonian strata, for which it may ultimately become a valuable index fossil.

INTRODUCTION

MACROFOSSIL evidence from sediments of the Lower Devonian has indicated that a relatively small flora existed at that time. In recent years, plant microfossil assemblanges have suggested that the flora was more diversified than was previously recognized (Radforth & McGregor 1954; Thomsom, 1952). In the present study, a preliminary investigation of the microflora from several specimens of rock disclosed several new taxa of plant spores. It has also suggested that many more plant species comprise the flora than is indicated by the macroflora.

The purpose of this paper is the description of a new genus of plant spores discovered In Lower Devonian strata from Gaspé Bay, Quebec. The apparent restriction of this form to Lower Devonian strata, together with its diagnostic characters, suggests that with further work, it may prove to be a valuable index fossil for the early Devonian.

The rock specimen was obtained from the Battery Point formation of the Gaspé Sandstone group of Eastern Quebec. The collection was made from beds containing *Psilophyton princeps* var. *ornatum* Dawson and other compression fragments. The age of the Battery Point formation has been determined as Lower Devonian by some workers, and Middle Devonian by others (McGregor 1959). Most recent opinions indicate a Lower Devonian age is most likely.

The plant microfossils were recovered from fine-grained sandstones, siltstones, and claystones. The treatment consisted of an initial maceration with hydrofluoric acid, followed by concentrated nitric acid. No alkali treatment was applied. Dispersion of microfossils was effected by employing a mixture of detergent and sodium carbonate, and subjecting the suspension to vigorous agitation. Slides were prepared using ordinary corn syrup as a mounting medium, following the method employed by Radforth and Rouse (1954), and Rouse (1957, 1959).

Many other spores in addition to the new genus have been identified. A frequency count indicated that the genus *Leiotriletes* is the most abundant (ca. 60%), whereas the genera *Trachytriletes*, *Lophotriletes*, *Hymenozonotriletes*, and *Archaeotriletes* are present in a much lower frequency (ca. less than 15%). The new genus, *Perforosporites*, has a frequency of approximately 3 percent. Specimens assignable to *Radiaspora* are represented, and minor constituents include species of *Acanthotriletes* and *Dictyotriletes*.

The material for this investigation was collected on a palaeobotanical excursion to Eastern Canada conducted for the IX International Botanical Congress in September, 1959. Acknowledgments are extended to Dr. D. C. McGregor of the Geological Survey of Canada, who conducted the excursion and made the collecting possible, and who also provided critical advice and assistance in the evaluation of the fossil material.

SYSTEMATIC DESCRIPTIONS

Super-Division SPORITES

Division TRILETES

Sub-Division AZONOTRILETES

Genus PERFOROSPORITES n. gen.

Genotype: *Perforosporites robustus* n. sp. (herein described).

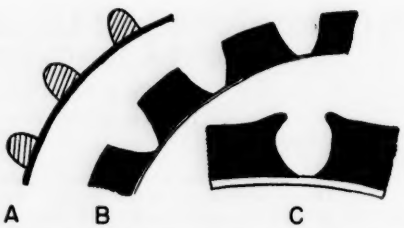
Generic diagnosis.—Trilete meiospores, roundly subtriangular in shape, with pores more or less evenly distributed throughout the distal surface of a thick wall. The pores

are circular to elliptical, crater-like, and are subtended by weak margins. In some specimens, the margins are sufficiently pronounced to appear as projections from the wall. The wall between the pores supports small, blunt papillae, which are sporadically distributed. The area of the wall covered by the pores is approximately one-third to one-half the total wall surface of the distal side. The pores appear to be concentrated on the distal surface, although several occur on the outer regions of the proximal surface.

Remarks.—In superficial aspect, spores of this genus are similar to *Dictyotriletes* (Naumova 1937) Potonié and Kremp, and were at first considered as a species of that genus. However, a closer appraisal of additional specimens has revealed that in *Perforosporites*, the pores appear to be circular to oval perforations in a thick wall. In contrast, species of *Dictyotriletes* have polygonal areas contained within a reticulum which is superimposed upon a thin wall (text-fig. 1). Some of the pores in *Perforosporites* appear to have thin membranous partitions stretched across the bottom of the pore, whereas others have complete perforations through the wall. The latter is suspected of being a result of preservation or chemical preparation treatment.

PERFOROSPORITES ROBUSTUS n. sp.
pl. 113, figs. 1–6; pl. 114, figs. 1–5

The general diagnosis of this species conforms to that given for the genus. The following attributes are considered to be additionally diagnostic for the genotype.



TEXT-FIG. *1*—Diagrammatic representations of the distinction in wall formation between *Dictyotriletes* and *Perforosporites*.
A. Idealized vertical section of the wall of *Dictyotriletes*, showing the reticulate thickenings (cross-hatched) on a thin wall (black).
B. Idealized vertical section of the wall of *Perforosporites*, showing the conical pores in a thick wall (black), and a thin basal layer of the wall (clear).
C. A diagrammatic view of a vertical section of one pore of *Perforosporites;* note the slightly overhanging margins of the pore which often give an appearance like a bordered pit when examined in plan view.

Size.—The observed size range of this species is 34 to 58 microns. The most common size ranges between 40 and 46 microns.

Shape.—Typical, undamaged specimens are roundly subtriangualr. The margin is generally smooth, but may be irregular where the margin intersects the pores (pl. 113, figs. 2,5 and 6).

EXPLANATION OF PLATE 113

FIGS. *1–6*—*Perforosporites robustus* n. gen. et sp., Lower Devonian, Battery Point formation, Grand Cap-aux-os, Gaspé, Quebec; University of British Columbia Palaeobotanical Collection, slides DLS 1–6. *1*, general view of the holotype, showing the oval to circular pores in the thick wall, ×1000; *2*, same specimen as fig. 1 with oil immersion, showing the depressions on the margin where the pores are intersected, ×2000; *3*, a specimen showing a weak trilete, the arms of which are indicated by the arrows. An overarching margin of a pore can also be noted off the end of the right-hand arrow, ×2000; *4*, a portion of the wall of the specimen in fig. 3, showing 2 pores in vertical section, ×2000; *5*, the same specimen as in fig. 3, taken at lower magnification to show the trilete suture, and notching of the wall off the arrow at the lower right, ×1000; *6*, a different specimen, showing a very faint trilete suture (arrows), and some of the papillae on the wall, ×2000.

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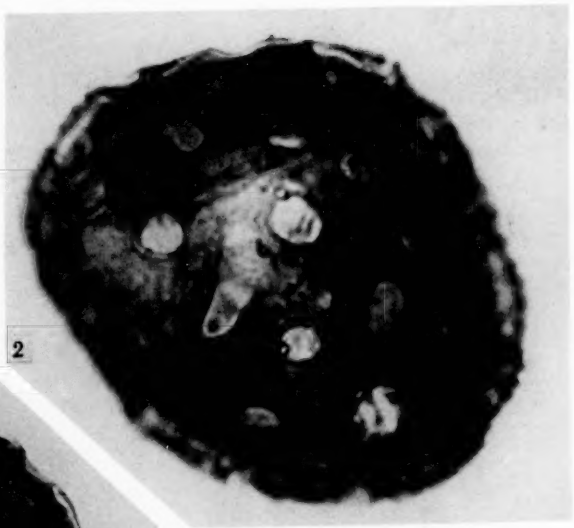
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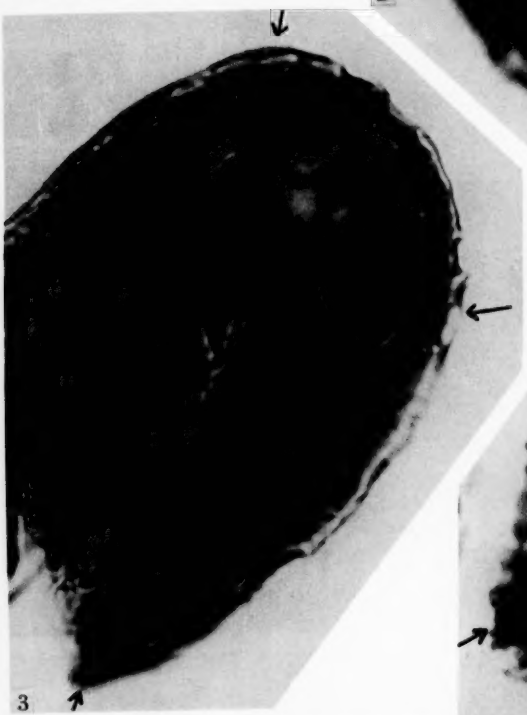
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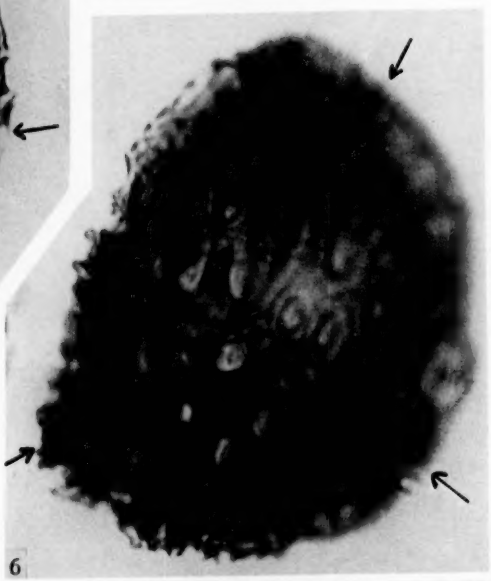
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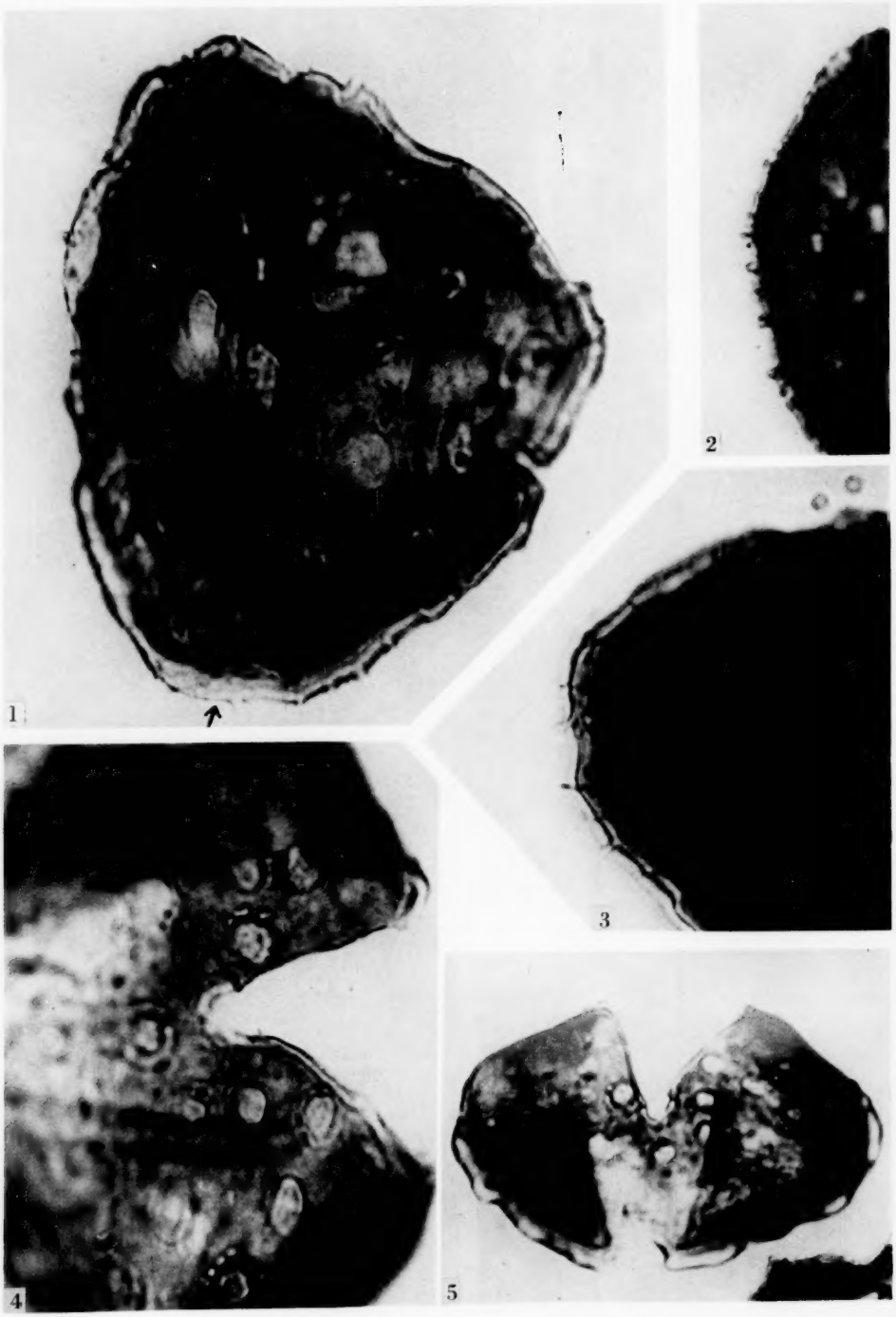
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Ornamentation.—Relatively large, distinctive pores or pits constitute the main surface ornamentation. The pores are evenly distributed over the distal surface, and have no systematic or preferred arrangement. The pores are circular to oval in shape, and constitute up to, but generally much less than, one half of the surface area. In most specimens, the pores range from 2.0 to 4.5 microns in diameter (pl. 113, figs. 1 and 2; pl. 114, figs. 1,4 and 5).

The pores are crater-like pits which seem to be floored with a very thin basal part of the wall. This makes the pores much lighter in colour than the surrounding body wall. A tiny black spot is commonly seen in the centre at the bottom of the pores; this is most likely an optical phenomenon. A ring-like margin, representing a thickening of the wall, surrounds some of the pores, and typically slopes gently away from the pore aperture (pl. 113, figs. 2 and 4). In some cases, this margin appears to project as an overhanging lip (pl. 113, figs 3 and 5). Where present, small protrusions along the margin appear to result from the projection of the rims of the pores, or of the body wall between the pores. In addition, short, slender, and blunt papillae are scattered sporadically on some specimens (pl. 114, figs. 1,2 and 3).

Haptotypic features.—Weak, thin, closed trilete rays can be noted extending to the margin. These have been observed on only a few specimens, but indicate a definite trilete pattern for the spore (pl. 114, figs. 3,5 and 6). As far as can be determined, the contact area is mainly devoid of pores.

Holotype.—pl. 113, figs. 1 and 2. The holotype is preserved on slide DLS-6, and permanently stored in the vault of the Department of Geology, University of British Columbia. The holotype is circled, marked with an arrow, and can be located at Ortholux co-ordinates 117.2 and 50.9.

Similar Forms.—Dictyotriletes insolitus McGregor (1957), pl. III, fig. 21,41–54 microns, Sextant formation, Lower Devonian, Abitibi River, Ontario.

Horizon and Locality.—Battery Point formation, Grand Cap-aus-os, North shore of Gaspé Bay, Quebec. Approximately 50′ below the crest of the sea-cliff, in projecting shale beds.

Discussion.—There is little doubt that *Perforosporites* and *Dictyotriletes* are distinct and separate form-genera. *Perforosporites* is characterized by having distinct pores in a solid body wall, whereas *Dictyotriletes* has a secondary reticulum superimposed on a primary wall (text-fig. 1). At first glance, there appears to be a pseudo-reticulate pattern to *Perforosporites*, which makes it appear superficially like *Dictyotriletes*. This similarity, however, is one of visual appearance only, and does not appear to be the result of any genetic relationship.

McGregor (1957) has reported a spore from the Lower Devonian Sextant formation as *Dictyotriletes insolitus* McGregor. This spore is apparently very similar to *Perforosporites robustus*, and possibly should be incorporated as a new species of this genus. However, McGregor indicated that a definite trilete mark was not present on any of the specimens encountered. The present

EXPLANATION OF PLATE 114

FIGS. *1–5*—*Perforosporites robustus* n. gen. et sp., Lower Devonian, Gaspé, Quebec. *1*, a general view of a subtriangular specimen, showing pores, papillate projections, and one arm of a faint trilete (arrow), ×2000; *2*, a view of a wall showing both knobbed and hooked papillate projections, ×2000; *3*, additional papillate projections on the wall, ×2000; *4*, an enlarged view of the central portion of the spore in fig. 5, showing the outline and arrangement of pores on one surface of the wall; the other surface has been split away, ×2000; *5*, a general view of a broken specimen showing pores on one surface and along the margin, ×1000.

authors consider it feasible to postpone the inclusion of *Dictyotriletes insolitus* McGregor in *Perforosporites* until additional information is forthcoming.

The evidence to date indicates that *Perforosporites* is restricted to strata of Lower Devonian age from North America. If this relationship continues in the future, *Perforosporites* may become a valuable index fossil, and may assist in the delimitation of Lower Devonian strata from those of Silurian, and Middle and Upper Devonian ages.

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Manuscript received June 15, 1960

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A COENOPTERID FERN FRUCTIFICATION FROM THE UPPER FREEPORT, NO. 7, COAL IN SOUTHEASTERN OHIO[1]

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ABSTRACT—*Monoscalitheca fasciculata*, a new genus and species, is described from compression material found in the shale parting of the Upper Freeport (No. 7) coal of southeastern Ohio. This fructification is allied to the family Zygopteridaceae of the order Coenopteridales. *Monoscalitheca fasciculata* consists of a very wide rachis which bears alternate distichous branches which in turn bear alternate circular sori. The sori are composed of numerous, elongated, curved, erect, free sporangia. Each sporangium has a single dorsally placed annulus which extends from the apex to the base of the sporangium. The cellular tissue to the left of the annulus differs from the tissue to the right of the annulus. The spores are numerous, small, rounded, trilete with scabrate ornamentation and would belong to the group *Punctatisporites* if found isolated.

INTRODUCTION

THIS paper, which is devoted to the description of a new coenopterid fern fructification from the shale parting in the Upper Freeport (No. 7) coal, is the first in a series designed ultimately to provide detailed descriptions of the flora found in the uppermost Allegheny strata of southeastern Ohio.

MATERIAL AND LOCALITY

The following description is based on compression material consisting of approximately thirty-six large specimens and many small specimens on shale, ten slides, and fifteen transfer specimens (see Abbott, 1950).

All the specimens were obtained by splitting a large block, 5×3×3 feet, of fine-grained micaceous shale. The fertile fragments were very close together vertically in the shale, but showed no relation to a larger axis.

Sterile foliage of the fern was not found. The following genera and species were found in intimate association with this fern fructification: *Sphenophyllum cuneifolium* (Sternberg) Zeiller, *Sphenopteris marrati* Kidston, *Mixoneura ovata* Hoffman, *Alloiopteris winslovi* D. White, and small aphlebiae attached to wide axes with stiff hairs up to 2 mm in length.

The types and figured specimens are catalogued in the Abbott Collection, Cincinnati, Ohio.

The specimens, upon which the study is based, were collected in a strip mine at Kimberly, Athens County, Ohio.

GENERAL DESCRIPTION

The larger, although incomplete, specimens measure 6–8 cm. in length, the rachis is 7 mm. wide at the base and narrows to 2 mm. wide toward the apex. This rachis bears thick alternate distichous branches giving a rigid rugose appearance to the plant (pl. 115, fig. 2). The alternate branches are 5 mm. apart throughout the length of the rachis. The longest, yet incomplete, branch is 6 cm. long and the other branches diminish in length as the apex is approached. The branches are attached at right angles to the axis and are 4 mm. wide and gradually diminish to 2 mm. wide near their apices.

Both the main axis and the lateral branches are composed of bright shiny coal which fractures evenly across the diameter of the axes. Reflected light shows a cellular pattern of the epidermis of the axes in which the thin walled rectangular cells are elongated in the direction of the length of the axis. No internal cellular detail can be established by thin sections, so that the relationship to any particuar coenopterid petiole cannot be determined.

The lateral branches bear alternate clusters or tufts of sporangia in a sorus (pl. 115, fig. 1). The sori are borne almost immediately on the acrostichous or lower side of the

[1] This work is a portion of a project supported by the National Science Foundation grant number G 9021.

branch as the branch leaves its larger axis. The sori are 3 mm. apart even up to the apex of the branch which terminates in a single sorus (pl. 115, fig. 1). The sori are oriented so that they are directed toward the apex of the lateral branches and are so close together that one slightly overlaps the base of the succeeding sorus. In no case are they lax or peltate.

The sorus consists of 10–16 free annulate sporangia which are circularly attached to the apex of a stalk. The stalk is 1 mm. wide even at the attachment of the sporangia and is as long as 4 mm., while those near the apex of a branch are only 2 mm. long. The attachment zone is not enlarged or thickened like the so-called sporangial pad of *Telangium* or *Crossotheca*.

The sporangia are free from one another through their entire length, even as they taper to their attachment to the stalk. The sporangia are from 3–5 mm. long with the more common length 4 mm. They are 0.75–1.00 mm. wide near their center and taper both apically and basally. Their apices are bluntly rounded. The sporangia are curved like a banana (pl. 115, figs. 1,3,4) with the annulate portion abaxial or directed away from the center of the sorus.

The multicellular annulus extends down the entire length of the adaxial side of the curved sporangium (pl. 115, fig. 3) and blends into the cells of the stalk. The annulus, as well as the entire sporangium, is one cell layer thick. The annulus is 6–14 cells in width throughout its entire length, although the maximum cell size makes it appear larger near the center of the sporangium and narrower as the cells diminish in size apically and basally.

The cell walls of the annulus are extremely thickened except where they are in contact with the parenchymatous tissue of the sides of the sporangium (pl. 116, figs. 4,5). Here, the three walls in contact with the annulus are very thick, while the fourth wall in contact with the parenchymatous tissue is as thin as the walls of the parenchymatous cells. The cells of the annulus are rectangular to pentagonal and average 28.4 mu wide and 56.8 mu long, although the shorter cells are 42.4 mu and the longest are 70 mu.

The tissue on the opposite sides of the sporangium is dissimilar. One side, to the left of the annulus (pl. 116, figs. 4,5), is composed of very thin-walled parenchymatous cells which are irregular in size and shape. The parenchymatous cells are interrupted by one or two groups of extremely small, rounded, sclerotic cells, clustered as in the stone cells of pears. The clusters contain 5–8 cells, each having a diameter of 10–12 mu or 51 mu across the cluster (pl. 116, fig. 4).

The opposite side of the sporangium, to the right of the annulus, is composed of two shapes and sizes of thin walled parenchymatous cells. The cells contiguous with the annulus and for several rows, up to as many as 18 rows, are elongated lengthwise from the apex to the base of the sporangium

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EXPLANATION OF PLATE 115

FIGS. *1–6*—*Monoscalitheca fasciculata* n. gen. and n. sp. *1*—portions of lateral branches showing the arrangement of the sori and the erect position of the sporangia in a sorus, specimen on shale, A 8000–8, mm. scale included; *2*—type specimen showing the overall robust appearance, wide rachises, and closely placed distichous lateral branches, specimen on shale, A 8000-1, mm. scale included; *3*—a complete sporangium with dorsal annulus extending from apex to base of 4 mm. long sporangium; *4*—reverse side of same sporangium showing narrow band of cells, at arrow, adjacent to annulus, for detail see pl. 116, figs. 1–2; maceration, preparation and photographs of figs. *3,4* courtesy of Dr. J. M. Schopf, U. S. Coal Laboratory, Columbus, Ohio, slide K 33, mm. scale included; *5,6*—individual rounded spores with short, distinct rays of trilete suture and scabrate sculpturing of spore coat, maceration, slide K 21, mu scale included.

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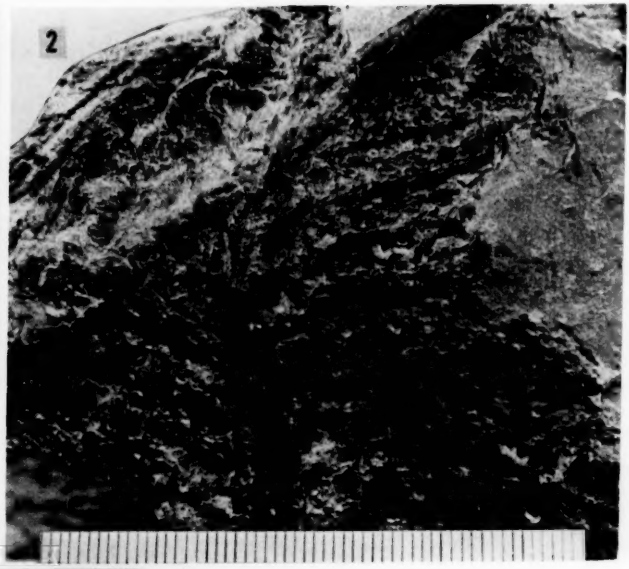
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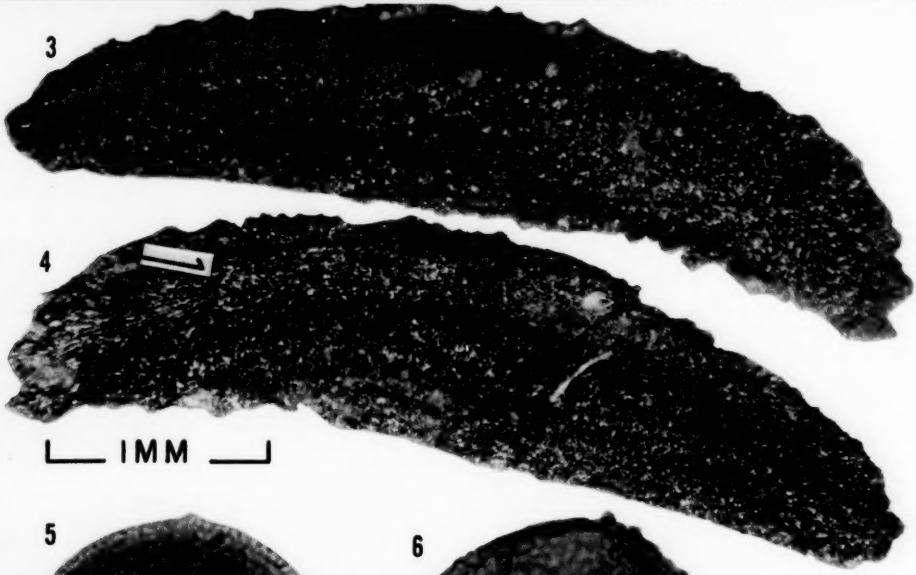
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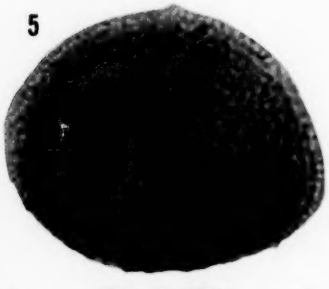
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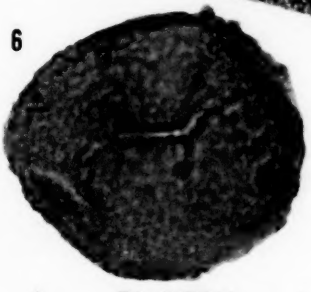
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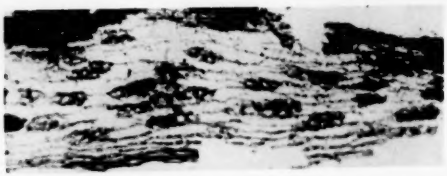
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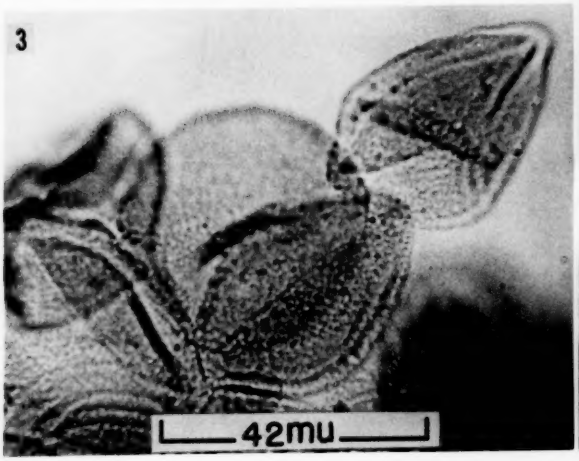
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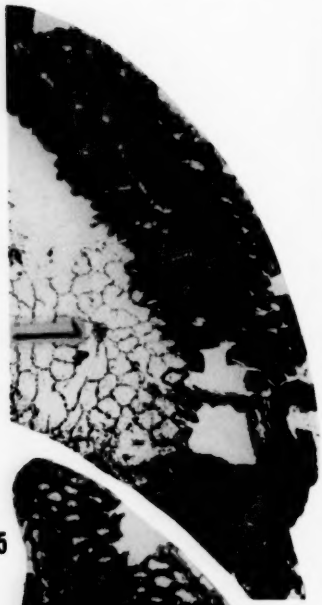
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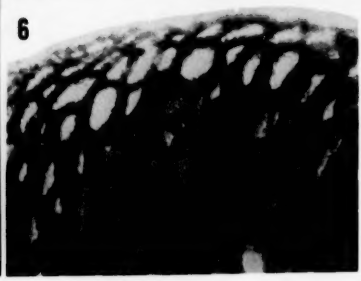
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(pl. 116, figs. 1,2). The cells are rectangular and average 21 mu wide and 57 mu long. These thin walled cells are interrupted very frequently by numerous scattered groups of dark colored sclerenchymatous cells. In size and shape, these cells are arranged much like the uni- or biseriate rays of a tangential section of wood (pl. 116, figs. 1,2). These groups are also oriented lengthwise with the long axis of the sporangium. They are uni- to biseriate in arrangement and are more or less rounded with extremely thickened walls, have dark colored contents, and measure 14.2 mu wide and 21.2 mu long. The cells adjoining this area as well as those of the remainder of the wall of the sporangium are irregular in shape and size and are like those to the left of the annulus.

The sporangia which were macerated contained a large number of small spores which were very difficult to separate even after prolonged maceration in Schultz's. The spore mass thus obtained retained the general banana-like shape of the sporangium which is probably due to an immature condition of the spores although no distinct tetrads were observed (pl. 116, fig. 3). Some spores were isolated and are 42.6–71.0 mu in diameter (pl. 115, figs. 5,6). They are spherical and have a prominent trilete mark with evenly spaced rays of equal length which average 15.6 mu. Some spores have rays as short as 14 mu while others have rays up to 17 mu in length. The spore surface is scabrate with dense circular elevations more or less 1 mu in height. The prolonged maceration perhaps reduced the granulose surface sculpturing of the exine. The spores fit into the *Punctati-sporites* group of isolated Paleozoic spores (Schopf *et al.*, 1944, p. 29, and Kosanke, 1950, p. 14). No endosporal cells were observed.

NOMENCLATURE

Since the sporangium of this coenopterid fructification is distinct, yet similar to that of *Biscalitheca* (Mamay, 1957), I propose the name *Monoscalitheca* for it thus referring to the single, dorsal, ladder-like annulus. The specific name *fasciculata* refers to the clustered or fascicled arrangement of the sporangia in each sorus.

SYSTEMATIC DESCRIPTION

Order COENOPTERIDALES Seward
Family ZYGOPTERIDACEAE Bertrand
MONOSCALITHECA FASCICULATA,
n. gen. n. sp.
Pl. 115, figs. 1–6; pl. 116, figs. 1–6

Generic diagnosis.—Rachis 2–7 mm. wide bearing alternate distichous branches 5 mm. distant; branches bear alternate circular sori 3 mm. distant; sori directed toward apex of branches; stalked sori composed of 10–16 free, erect sporangia; sporangia elongate, curved, annulate; walls of sporangium one cell layer thick; annulus multicellular, extending from apex to base of sporangium and adaxially placed; thin walled cells to the left of annulus irregular in size and shape; several rows of thin walled cells to the right of annulus elongated with the long axis of sporangium and interrupted by numerous scattered "ray" shaped groups of smaller sclerenchymatous cells; farther away from the annulus the parenchymatous cells are irregular in size and shape; spores small,

EXPLANATION OF PLATE 116

FIGS. *1–6*—*Monoscalitheca fasciculata*, n. gen. and n. sp. *1,2*—an enlarged portion of the narrow band of elongated parenchymatous cells and elongated groups of sclerenchymatous cells from approximately the same area on another specimen as that shown by arrow on pl. 115, fig. 4, transfer, slide K 26, 1—×300, 2—×50; *3*—a portion of the edge of a sporangial mass showing compactness of spores and scabrate sculpturing of spore walls, transfer, slide K 21, mu. scale included; *4–6*—enlarged portions of left side of apex of sporangium to show details of ladder-like arrangement of cells in annulus, thin walled irregular cells of sporangium wall, and at arrow, a rounded cluster of extremely small, thick walled cells which occur only occasionally on this side of sporangium, transfer, slide K 26, 4,5—×50, 6—×100.

rounded, trilete with scabrate sculpturing. Vegetative parts unknown.

Specific diagnosis.—Pedicellate sori 3 mm. distant on thick lateral branches, alternate, distichous, contain 10–16 annulate, free sporangia. Sporangia 3–5 mm. long, 0.75–1.0 mm. wide near center and taper to base and to blunt rounded apex. Sporangia gently curved with the annulus occupying the center of the convex adaxial side from apex to base, and directed to outside of sorus. Sporangium one cell layer thick; annulus 6–14 cells wide, cell walls extremely thickened, cells rectangular to pentagonal, average 24.8 mu wide and 56.8 mu long. Sides of sporangium composed of 2 cell types; side of sporangium to left of annulus composed of irregular, thin-walled parenchymatous cells, interrupted once to not more than three times by rounded groups of 5–8 extremely small, rounded, sclerotic cells 10–12 mu in diameter; side to right of annulus composed of several rows of thin-walled elongated rectangular cells adjacent to the annulus; farther away from the annulus the cells are irregular in size and shape and similar to those on left side of annulus. Elongated rectangular cells are 21 mu wide and 57 mu long, interrupted by numerous scattered "ray" shaped groups of sclerenchymatous cells; sclerotic group of cells uni- to biseriate in arrangement and 2–10 cells in length or 14.2–21.4 mu wide and 21.2–140.0 mu long. Spores numerous, rounded, trilete, 42.6–71.0 mu in diameter; trilete mark prominent with evenly spaced rays of equal length averaging 15.6 mu; spore sculpturing scabrate with dense circular elevations more or less 1 mu. in height. No endosporal cells. Spores referable to *Punctati-sporites* if found isolated.

Remarks.—*Monoscalitheca* is more closely allied to the genera included in the family *Zygopteridaceae* of the order *Coenopteridales* than to any other group of Paleozoic ferns. Six fructification genera are placed in this family. Three are described from compression floras: *Corynepteris* Baily, *Etapteris laccatei* Renault, and *Monoscalitheca*. Two are described from silicified or coal ball floras: *Notoschizaea* Graham and *Biscalitheca* Mamay. *Zygopteris* Corda has been described from both compression and petrified material.

Monoscalitheca differs from *Corynepteris* and *Notoschizaea* in that these two genera have closely adherent sporangia in a sorus which occurs on more or less modified pinnules. No foliage in direct connection was found on *Monoscalitheca*. *Monoscalitheca* differs from the other genera bearing free sporangia of the same general shape and size, which are clustered into a sorus, since most of these genera are exannulate, e.g. *Telangium*.

In *Zygopteris pinnata* Grand'Eury as reported by Zeiller, 1888, there are 3–10 sporangia in a sorus; in *Z. cornuta* Zeiller, 6–12; in *Zygopteris* sp. Remy, 6–8; in *Etapteris laccatei* Renault, 3–8; in *Biscalitheca* Mamay, not known; in *Monoscalitheca* 10–16.

In its over-all appearance, *Monoscalitheca fasciculata*, with its wide rachis and rigid, robust appearance, is remarkably similar in gross features to Renault's *Etapteris laccatei* which he described in his Commentry Flora. Although there are fewer sporangia in the sorus of *E. laccatei*, the greatest dissimilarity is found in the cellular details of the sporangia. *E. laccatai* is biannulate and the sporangial wall is several cell layers in thickness (see Renault, 1876, and Hirmer, 1927), while in *M. fasciculata* there is only one annulus which is dorsal and extends from the apex to the base of the sporangium and the sporangial wall is one cell layer in thickness. As *M. fasciculata* is different from *E. laccatei*, it also differs from all the other species in this general group since they also have two annular areas variously placed on the sporangial wall. With the exception of *Biscalitheca*, the other genera under discussion also have more than one layer of cells comprising their sporangial walls. Remy (1955) did not give cellular details of the sporangial wall of *Zygopteris* sp.

Even though the sporangial walls of *Biscalitheca* and *Monoscalitheca* are one cell layer in thickness, they differ in cellular detail. The annular cells of the two genera are much the same in size, in shape and arrangement, that is "ladder-like." The three areas of sporangial walls of *Biscalitheca*, other than the two annular areas, are similar in that they are composed of elongated thin walled parenchymatous cells frequently interrupted by sclerenchymatous groups (see Mamay, 1957, fig. 30). *Mono-*

scalitheca has two areas of sporangial wall only one of which is prominently interrupted by sclerenchymatous cell groups, while the other is composed of irregularly shaped parenchymatous cells and interrupted only once or twice along the entire wall by very small, 10–12 mu in diameter, rounded sclerenchymatous cells in rounded groups of 6–8 cells (pl. 116, fig. 4).

The spores of the six genera have been described in detail and if found isolated would fall within the circumscription of *Punctati-sporites* (Schopf *et al.*, 1944). Remy (1957) placed the spores of several species of *Zygopteris* in the group *Verrucosisporites* Potonié & Kremp; however, according to the rules of International Botanical Nomenclature this term must be placed in the synonomy of *Punctati-sporites*.

The spores of Zygopteridaceae are trilete and those with the most ornate sculpturing belong to genus *Zygopteris*. In these the exine is described as granulose and verrucose. The spores belonging to *Biscalitheca* are also ornate but to a lesser degree than the species of *Zygopteris*. These spores are favorably compared to those of *Osmunda regalis* (prepared from Herbarium sheets, University of Cincinnati). The spores of *Corynepteris silesiaca* Remy, R. & W., 1955, are like the spores of *Monoscalitheca fasciculata* (pl. 116, fig. 3; pl. 115, figs. 5,6). According to Graham, 1934, the spores of *Notoschizaea robusta* are smooth and trilete, thus making them the least ornate of all the genera.

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EARLY ONTOGENY IN THE TRILOBITE FAMILY ASAPHIDAE

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ABSTRACT—The morphology and development of protaspides representing the family Asaphidae are described from silicified specimens etched from Middle Ordovician limestones of northern Virginia. Close similarities with remopleuridid protaspides described by Whittington and Ross suggest that the Asaphidae and Remopleurididae are more closely related than generally has been recognized. The asaphid protaspides represent early stages of the protaspid period, before complete differentiation of a protopygidium. For an unknown reason, the late protaspid period is not represented among the fossils, although early meraspid stages are common. The resultant "missing" interval in the recorded asaphid ontogeny appears to be the interval best represented by known remopleuridid protaspides. Evidence for and some implications of this interpretation are discussed.

INTRODUCTION

General.—The purpose of this paper is to describe the type of protaspis that occurs in the trilobite family Asaphidae. Asaphids younger than the meraspid period (Whittington, 1941) have not been described previously. Originally I intended to describe the protaspid development as part of a larger study of the asaphid genera and species that occur in silicified residues of acid-etched Middle Ordovician limestones from the Shenandoah Valley, Virginia. The asaphid protaspides are now being described separately in order not to delay further the publication of observations on these interesting specimens. Papers describing other components of these assemblages of silicified trilobites include those by Cooper (1953), Evitt (1951, 1953), Evitt and Whittington (1953), Whittington (1941, 1949, 1956, 1959), and Whittington and Evitt (1954).

Although the majority of specimens encountered probably represent *Isotelus*, the general term "asaphid" is used throughout the discussion. I have not yet attempted the extensive study of all available specimens that would be required to analyse the slight differences among the species and genera probably present, and to match the extremely similar meraspid stages with their holaspid counterparts. An even greater challenge (in fact, probably an impossibility with presently available material, extensive though that is) will be to match the protaspides with their respective meraspid series. This is because of a conspicuous gap in the early ontogeny as recorded by the silicified specimens. The gap occurs in the late protaspid period. It appears to be characteristic of the genera represented by these specimens and not to result from sampling, current sorting, or other processes unrelated to the organisms themselves. Perhaps it is a family-wide trait.

Material and localities.—Material from the Lincolnshire, Edinburg, Oranda and Martinsburg formations at numerous localities in the Shenandoah Valley (including most of those listed by Whittington, 1959, and others in addition) was used in this study. I believe it is correct to say that none of the blocks from any of these units that yielded more than a few silicified trilobites failed to yield protaspides of the sort described here. The descriptions and interpretations offered are based on the collective evidence of all the specimens studied. However, all the figured specimens came from the following four localities:

Locality 1. Lower part of Lincolnshire limestone (Bed 3 of Cooper and Cooper, 1946, Geologic section 10, p. 76), in the interval between 20 and 24 feet above the contact with the underlying New Market limestone. Exposure is in road cut along north bank of Tumbling Run, 2 miles southwest of Strasburg, Shenandoah County, Virginia.

Locality 3. Lower part of Edinburg limestone, section in field on south side of road, 0.2 mile east of Strasburg Junction, just west of Strasburg, Shenandoah County, Virginia. These beds seem to be the basal Botetourt limestone member of the Edinburg formation.

Locality 4. Botetourt member, lower part of Edinburg limestone, in upper part of field northeast of Virginia secondary highway 639, at a point 0.25 mile from its junction with U. S. Highway 11. This junction is 0.7 mile southwest of Strasburg, Shenandoah County, Virginia. The outcrop is approximately half a mile southwest of locality 3 along the strike of the beds.

Locality 10a. Limestone beds in lower part of Martinsburg formation at extreme west end of north-facing hillside exposure, about 0.25 mile southwest of locality 10 (Whittington, 1959, p. 383), which is on Virginia secondary highway 772 about 1 mile east of Greenmount Church, 0.5 mile west of junction with Virginia Highway 42, and 5 miles north of Harrisonburg, Rockingham County, Virginia.

Whittington (1959) gives additional data on these localities (except 10a) and lists many of the trilobite faunas known from the middle Ordovician sequence of the Shenandoah Valley.

Figured specimens are in the U. S. National Museum.

Acknowledgments.—My wife sorted from the fine residues the majority of specimens on which this study is based. She was the first to suspect the true association of parts of the asaphid protaspid, and then to find the specimens that proved the case. Her many hours patiently before the microscope and her keen eye for small strange objects made this paper possible. I am also indebted to Dr. G. Arthur Cooper and Dr. H. B. Whittington for the material collected and prepared by them that was used in this study. Publication is with the permission of Jersey Production Research Company.

How the asaphid protaspis was recognized.—When Dr. H. B. Whittington, Dr. R. J. Ross, Jr., and I first began to study silicified Ordovician trilobites intensively, we found many "problematica," both trilobites and non-trilobites. Gradually, evidence for the identification of most of these was pieced together. Strangely, some of the most baffling specimens were both abundant in and common to many of our samples, ranging throughout the section we were collectively studying from Canadian to Trentonian in age. Particularly puzzling were objects I referred to as "crowns of thorns" (pl. 118, figs. 30,34). In Ross' material from Nevada these were commonly adorned with two crescentic projections; most of those from Virginia were plain. Other peculiar objects that occurred in symmetrical counterparts and varied sizes (pl. 118, figs. 10,13) we dubbed "bananas" in Virginia. A third type of strange object, abundant in some samples, was a nearly smooth, strongly convex, hollow structure with pairs of large spines (pl. 117, figs. 1–18). At first we were uncertain that these were actually parts of trilobites. Slowly we became sure they were. We eventually recognized the smooth convex object as a new type of protaspis, the "crown of thorns" as a minute hypostome, and the "bananas" as tiny free cheeks, sometimes attached to the hypostome and sometimes separate. Ross (1953, p. 645, pl. 63, figs. 21,22) described and briefly discussed this type of hypostome with its attached cheeks, mentioning our suspicion (now proved erroneous) that it might belong to a dimeropygid. Gradually, as we recognized their similarity of outline along the facial suture, we came to suspect that the crescentic free cheeks went with the convex protaspis. Only much later, however, after amassing many hundreds of specimens, did we find the one specimen (pl. 117, fig. 19) that proved the case—a convex protaspis with two free cheeks and hypostome almost in their original position.

Study of the large assortments of specimens soon showed that they represented a developmental series within the protaspid period. This progressed from the early stages, in which cheeks and hypostome were fused, to later ones in which the three parts were separate, the cheeks being divided by a median suture. So much we knew, but we still had no idea what trilobite was represented. Especially puzzling was the lack of transitional forms leading from this protaspis to meraspid specimens of identifiable genera. Although this lack remains a problem that is discussed at the end of this paper, a process of elimination gradually pointed to the Asaphidae as the trilobite family involved. This was the only family with unknown protaspid morphology that was represented in all the assemblages containing the mysterious protaspides. The conclusive evidence was provided by a sample of Tren-

tonian age (Martinsburg formation, locality 10a) with a very limited trilobite fauna. In this material the unknown protaspides were abundant, along with meraspid and holaspid individuals (likewise abundant) of only three trilobites: a cheirurid, a calymenid, and an asaphid.

DESCRIPTION AND DISCUSSION

Before proceeding to a detailed description of the protaspis and its development, a brief characterization of the main features of the structure may be helpful. The reconstructions (text-figs. 1–3) will aid in orientation.

The protaspis consists in principal of a hollow, partial sphere in which access to the interior is restricted by a relatively large and conspicuous spinose hypostome. The facial suture is well developed in the earliest stages. The hypostome is at first fused with the free cheeks to make a single structure, chiefly ventral in position. These parts later become separated by median and hypostomal sutures. The visual surface of the eye is not apparent, but the eye's position is indicated after the earliest stages by the course of the suture. Early stages are externally smooth; later, anterior pits and faint axial furrows appear on the cephalon, and faint transverse furrows may mark four or five segments of the protopygidium. Prominent paired anterior and posterior spines are present.

Earliest protaspis found.—Whole structure (pl. 117, figs. 1–4; text-fig. 1) subhemispherical, longitudinal convexity somewhat greater than transverse; outline in plan view flattened across front, strongly convex behind; about 0.7 mm. long. Pair of short, divergent horizontal spines mark rounded anterolateral corners just above suture. Pair of similar spines, more closely spaced, project obliquely downward, backward and outward beneath posterior extremity. Cheeks and hypostome fused into single, chiefly ventral structure (pl. 118, figs. 5–7). Cheeks visible from front and side as narrow band; suture forms gently sinuous upper limit. Suture curves under to ventral surface at about two-thirds the length, meeting edge of doublure about even with posterior end of hypostome. Hypostome as a whole broad and flat, main portion subcircular in outline. V-shaped central body has faint, independent transverse convexity, but flares smoothly forward into cheeks (pl. 118, figs. 22–26); tapers back to rounded posterior projection. Lateral lobe slightly depressed, surmounted by four long spines that project obliquely downward and outward across crescentic opening between free margin of hypostome and cheeks. Lateral hypostomal borders nearly vertical, flared and thickened slightly at free margin, without distinct doublure. In lateral view of some specimens (pl. 118, fig. 23) this border tapers to disappear where median lobe flares into cheek; in others (pl. 118, fig. 26) a rudimentary anterior wing is recognizable at this point. Free edge of free cheek turned sharply up to form narrow vertical doublure. Externally no indication of anterior pits or furrows of any kind.

Latest protaspides found.—Characteristics of this stage (text-fig. 3) are stated below, chiefly as a list of contrasts with or changes from the stage just described.

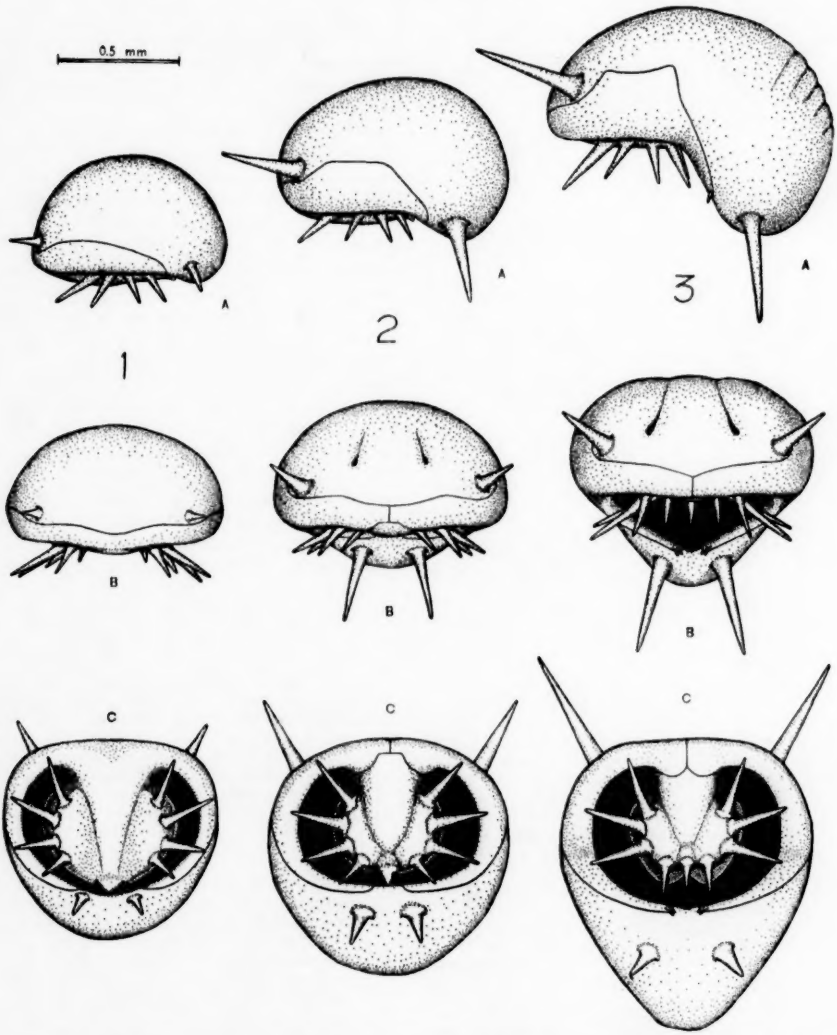
1. Larger (maximum dimension about 1 mm.), particularly in posterior part where effect of differential growth is especially apparent in side view. In some specimens traces of segmentation visible here (pl. 117, fig. 18).

2. Pair of elongate anterior pits continue rearward as faint axial furrows, thus differentiating glabella. No transverse segmentation of glabella apparent. Posterior limit of chephalon not marked.

3. Facial suture behind anterolateral cranidial spine has markedly different course (pl. 118, fig. 4). This causes relative increase in area of free cheek and clearly defines position of eye and palpebral lobe. No trace of visual surface (pl. 118, fig. 15); no portions of ocular region have independent convexity.

4. Free cheeks separated at front by short, straight median suture and from hypostome below by doubly arcuate hypostomal suture (pl. 118, figs. 13,14,30,33).

5. Posterior branch of facial suture behind palpebral lobe runs downward, under and inward almost to posterior midline, then makes short cut at acute angle to free margin (pl. 117, figs. 15,16). Posterior ends of the two sutures thus isolate a distinctively shaped median structure (pl. 117, fig. 15; text-figs. 3b,4c) that includes obtuse pos-

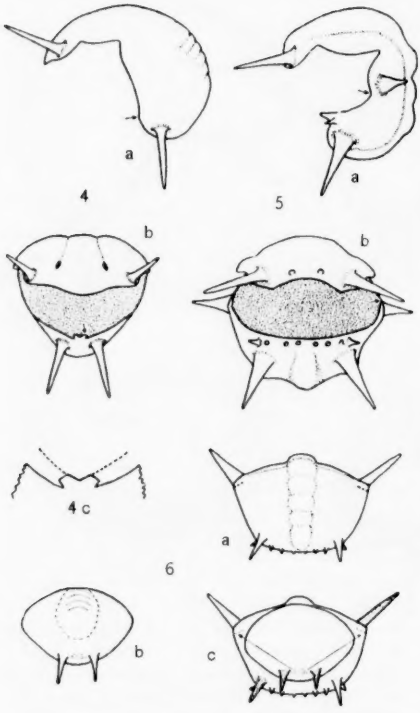


TEXT-FIGS. *1–3*—Reconstructions of three stages in the protaspid development of asaphid trilobites; a, left lateral view; b, anterior view; c, ventral view. *1*—Earliest protaspid stage found; *2*—Intermediate stage; *3*—Latest protaspid stage found; believed, however, still to represent a relatively early part of the protaspid period.

terior extremity of ventral opening.

6. Minute genal spine apparent as projection from posterior extremity of free cheek (pl. 118, figs. 9,14; text-fig. 3).

7. Hypostome (pl. 118, figs. 30–34; text-fig. 3c) relatively smaller with respect to the ventral opening. Median lobe with moderate independent convexity, lateral lobes



TEXT-FIGS. *4–6*—Comparison between protaspides of Asaphidae and Remopleurididae. *4*—One of latest known asaphid protaspides, without free cheeks and hypostome. *4a*—Left lateral view. *4b*—Anterior view. *4c*—Detail of structure between posterior extremities of facial sutures shown in 4b and, by dotted lines, in 6b and 6c; dashed line in 4c shows position of inner edge of free cheeks.

5—Protaspides of *Remopleurides caelatus* Whittington. *5a*—Left lateral view, after Whittington (1959, text-fig. 4c). *5b*—Anterior view, after Whittington (1959, text-fig. 4a).

Comparison of text-figs. 4 and 5 shows the much more advanced stage of development represented by the remopleuridid protaspides. Note, also, the two pairs of large spines in the asaphid and the three pairs in the remopleuridid. The small arrows show where the posterior branch of the facial suture crosses the doublure at the posterior extremity of the free cheek.

6—Diagrams to illustrate differences in the protopygidium in known asaphid and remopleuridid protaspides. *6a*—*Remopleurides caelatus* Whittington, exterior view of protopygidium (based on Whittington, 19,59 pl. 3, fig. 3), showing large axial segments, posterior pair of protopygidial spines, pleural spines of four segments along posterior margin, distinct posterior limit of cranidium, large fixigenal spines projecting from cranidium at upper corners. *6b*—Asaphid protaspis, exterior view of posterior portion of protaspis (based on pl. 117, figs. 9 and 18 in this paper), showing large pair of posterior spines, between them (on the inner surface and therefore dotted) the characteristic median structure between ends of sutures, rudimentary protopygidial area (enclosed in dashed line) with indications of several small segments along axis. *6c*—Superposed outlines shown in 6a and 6b (without axial detail) to show alternative interpretations of relationships of major spines. On the left, shading indicates homology of posterior spine of asaphid with posterior spine of remopleuridid. On the right, posterior spine of asaphid is homologous with fixigenal spine of remopleuridid. Arrows show migration, during growth between intermediate (asaphid) and late (remopleuridid) protaspid stages, of point where posterior branch of suture crosses doublure. The right-hand interpretation is favored because spine and suture-crossing maintain same relationship and migrate together.

more strongly convex; latter formed essentially of fused bases of lateral spines. Spines longer and stouter than before; posterior median projection now a spine similar to lateral ones, but shorter. Lateral border vertical, wide; flared and thickened at free margin, except where distinct median posterior notch is developed. At anterolateral corner, lateral border is drawn forward and upward into long thin anterior wing of suitable design to contact inner cranidial surface at anterior pit, although no specimens in actual contact have been observed.

8. Paired anterior and posterior spines are longer and more massive.

The illustrations show the shapes of the separated and assembled parts of the protaspides in the two stages just described, as well as in intermediate stages. Comparison of the illustrations will reveal the principal changes that took place during the part of the protaspid period recorded by these specimens. Pl. 117, fig. 19 and pl. 118, figs. 37,38 show one of the very rare examples in which more than one of the skeletal parts of a single

protaspis, although slightly displaced, are preserved in their original association.

Discontinuity in the ontogenetic series.— Thousands of specimens have been found that represent the protaspid stages described above. Skeletal parts representing the early meraspid period (compare Whittington, 1941, pl. 75, figs. 27–29,34–39) are much less abundant (although not rare), and specimens that nicely bridge the gap from the typical protaspis to the typical meraspis have not been found. Changes in all parts of the exoskeleton from the early meraspid configuration to the holaspid are gradual, and are amply documented by intermediate stages. Not so the changes from the protaspid to the meraspid. The meraspid characters are reviewed briefly in the following paragraphs.

Small meraspid cranidia (about 2 mm. long) (pl. 117, figs. 20–23) show features not greatly different from much larger individuals. Although specific characters are perhaps not yet recognizable and generic traits are not clear, the family characteristics are distinct. A nearly complete specimen of meraspid degree 1 (lacking only the hypostome) has a cranidium closely comparable to the two figured here, which are only slightly larger. The chief contrast with holaspid specimens is the more abrupt change in surface contour that outlines the glabella. Free cheeks are also generally similar to much larger ones.

In the case of the hypostome, one specimen (pl. 118, fig. 35) comes fairly close to bridging the gap between the distinctive hypostome of the late protaspis and the equally distinctive, but very different one of the holaspis. The hypostome at this stage had lost the radiating spines so conspicuous in the protaspis, as well as the doubly arcuate hypostomal suture and the long anterior wing. Also, the pair of posterior prongs and the deep reentrant between them are like the holaspis. However, the principal lobes and furrows of the protaspid structure can still be identified. These are not present in the holaspid specimens (pl. 118, fig. 36).

Meraspid pygidia (Whittington, 1941), especially of early degrees, are quite distinct from holaspid ones. They are more convex, have a more clearly defined axial lobe, and much clearer segmentation. In addition, a sharp notch, absent in the holaspis, marks the midpoint of the posterior margin. However, changes to the holaspis are gradual, and the same features that distinguish the young meraspid pygidium from the holaspid one distinguish it also from the posterior portion of the known protaspides.

In contrast to the gradual changes recorded in the development from early meraspis to holaspis, the latest known protaspides are markedly different from the earliest meraspid specimens. Five outstanding differences are the following:

1. The outline shape and the convexity of all the principal parts of the exoskeleton are strikingly different in the latest protaspis found and the earliest meraspis.

2. In all the protaspides the paired anterior and posterior spines are prominent, but no trace of them appears in any of the meraspid specimens.

3. Although the position of the palpebral lobe is apparent except in the earliest protaspides, none of the free cheeks shows any trace of a visual eye surface, whereas a convex visual surface similar to that in the holaspis is prominent in young meraspid cheeks. The outlines of the free cheeks and the genal spine are also completely different.

4. The posterior portion of the protaspis shows a basic difference in structure from the transitory pygidium. In the late protaspis the posterior tips of the two free cheeks almost meet on the under side at the posterior midline, even though in some cases (only in specimens from locality 10a, possibly representing a single species) a number of protopygidial segments can be identified on the axis and flanks of the external surface. This means that the protopygidium, although consisting of several segments, was almost, if not entirely out of contact with the free margin. It had no doublure, and was effectively surrounded by elements of the cephalon. In contrast, the earliest transitory pygidia are approximately semicircular in outline, with a wide doublure running the length of the arcuate free margin.

5. The doublure in all the protaspides is feebly developed. Except around the hypostome, where it is virtually absent, it is represented by a very narrow band turned under approximately at right angles to the adjoining external surface (e.g., pl. 118, figs. 16,17,

19,20). In contrast, the broad and relatively flat doublure, about parallel to the external surface, that is well known in holaspid specimens of asaphid genera, is also characteristic of the meraspid stages.

The explanation of the discontinuity in the development as recorded by the series of specimens is not clear. In part, the lesser abundance of specimens of older animals reflects selective preservation, for the large, flat and relatively thin parts of the meraspid and holaspid exoskeletons are mechanically much weaker than the compact, convex, and relatively thicker structures of the protaspis. But this does not adequately explain the apparently complete gap in the record. Sorting by shape and size through current action is a conceivable cause, but can be excluded when one considers that the "missing" stages could hardly have differed more in shape and size from the parts that have been found than these do among themselves. Failure to recognize the "missing links" is another possible explanation. However, it is not a plausible one in light of the occurrence of parts of both younger and older individuals and the distinctiveness of their features. I can say confidently that any parts with a transitional morphology must be exceedingly rare to have escaped detection during the intensive search made for them in the many samples examined.

Having dismissed preservation, sorting, and the "human element" as unable to provide a satisfactory explanation of the discontinuity in the observed growth sequences, two other possibilities may be mentioned:

1. Perhaps the young asaphid passed through a sort of metamorphosis, during which greatly accelerated development was incompletely recorded in molted exoskeletons.

2. Perhaps the growing trilobite was adapted during the "missing" period, to a particular activity and habitat (e.g., burrowed in the mud) different from its earlier and later stages. Possibly it was without hard parts, or its specialization somehow precluded preservation of its exoskeleton along with those from earlier and later stages.

Neither of these phenomena is known to have occurred in the ontogenies of other trilobites, and no direct evidence currently available seems to bear on either one as applied to the present case of asaphid ontogeny.

Comparison with protaspides in the family Remopleurididae.—Whittington (1959, p. 397) drew attention to resemblances between the protaspides of *Menoparia* and *Remopleurides*, which he considers to represent two subfamilies of the Remopleurididae. These are the only described protaspides that are closely similar to the asaphid forms described here. The similarity, obvious if one refers to the illustrations of Ross (1951) and Whittington (1959), is emphasized by consideration of undescribed protaspides of *Remopleurides* (probably *R. eximius* Whittington) that represent earlier stages than any described by Whittington (1959). These will be the subject of a future discussion. They demonstrate that in the early remopleuridid, as in the asaphid, the free cheeks and hypostome were fused into a single unit.

This asaphid-remopleuridid type of protaspis has the following characteristics that, in combination, set it apart from other described types: Relatively large (up to 1 mm.); extremely convex, both longitudinally and transversely; external contours broadly rounded; glabella faintly (or not at all) delimited by axial furrows, without indication of segmentation; anterior border and eye ridges not apparent; palpebral lobes without independent convexity, denoted by course of suture behind pair of conspicuous spines at anterolateral corners of cranidium; a second pair of spines on posterior part of protaspis (and, in *Remopleurides* and *Menoparia*, a third pair near sides at mid-length); free cheeks and hypostome in early stages fused into single relatively large unit covering most of ventral surface, later divided by sutures.

The phraseology of this characterization is general in order not to become involved in distinctions between early and late protaspides for which there is still insufficient evidence. Revision or elaboration will be required by additional information.

To what conclusions regarding possible relationships between the Asaphidae and Remopleurididae do these observations lead us? At this juncture our still limited knowledge of trilobite protaspides and the signifi-

cance of their similarities and differences urges caution. However, an important generalization seems to be taking shape: similar protaspid morphology in many instances is a good clue to close familial relationship. This seems to be borne out by the described protaspides that now represent many families and genera (reviewed by Whittington, 1957) and by extensive unpublished material in the collections of Dr. Whittington and myself. Therefore, the possibility that the Asaphidae and the Remopleuridiidae are much more closely related than has generally been assumed from their holaspid morphology should be carefully explored.

In comparing the protaspides of *Menoparia* and *Remopleurides* on the one hand with those of asaphids described here on the other, a feature in addition to their basic similarity is apparent: the recorded ontogenetic series of *Menoparia* and *Remopleurides* seem to begin at a later stage, at least so far as the development of the protopygidium is concerned. In fact, the described protaspid stages in those two genera show precisely the characters one would expect in the ontogenetic interval described above as "missing" in the asaphid record. Although the explanation of this is not apparent, a brief discussion seems worthwhile.

Text-figs. 4 and 5 show the chief features of one of the most advanced asaphid protaspides and of a remopleuridid protaspis. Special points of interest are the following:

1. The size and convexity of the protopygidium.
2. The degree to which the protopygidium is differentiated from the cranidium.
3. The spacing of the two large posterior spines, the number of protopygidial segments indicated by marginal spines between them, and the distance separating the points where the posterior branches of the facial sutures cut across the doublure.
4. The degree of similarity of basic protaspid elements (cranidium and protopygidium) to their early meraspid equivalents.

Considering these points, we note that the most advanced asaphid protaspis appears much less fully developed than the remopleuridid. This is especially clear in the protopygidium, which is relatively much smaller and less convex (longitudinally). The large posterior spines are close together. No traces of protopygidial segments exist along the free margin between them where, in fact, the ends of the facial sutures almost meet. The division between cranidium and protopygidium is not clear, except along the axis. In short, the protopygidium seems to be in an early formative stage, in which differentiation of its segments has proceeded only along the axial region and immediately adjacent pleural areas.

In sharp contrast is the well-formed protopygidium in *Remopleurides*, clearly differentiated from the cranidium, with large posterior spines separated by pleural spines representing several segments, and a longitudinal convexity that brings the posterior extremity of the protopygidium close to the anterior extremity of the cranidium.

Furthermore, in *Remopleurides* (e.g., Whittington, 1959, pls. 3 and 10) and in *Menoparia* the cranidium and protopygidium of the late protaspis differ from those of the early meraspis only in that they are still fused. No discontinuity in the recorded development exists.

The comparisons made above emphasize the discontinuity in the recorded asaphid ontogeny pointed out earlier. By suggesting that the fossil records of trilobite ontogenies may begin at different levels of development in different genera, they also agree with observations made elsewhere. For example, Evitt (1953) and Whittington and Evitt (1954) have noted that in the cheirurid genera, *Ceraurus*, *Ceraurinella* and *Sphaerexocus*, the earliest stages found represent a much later ontogentic level of development than in the closely related genus *Acanthoparypha*. In *Ceraurus* and *Sphaerexochus* the earliest pygidia that occur commonly are transitory ones about halfway through the meraspid period (degree 5 or 6); in *Ceraurinella* the earliest known stage is degree 0. In contrast, protaspides with small protopygidia (Whittington and Evitt, 1954) and even very early protaspides without indication of protopygidia (unpublished observation) are known in *Acanthoparypha*.

A further point of contrast between the asaphid and remopleuridid protaspides is

instructive. In the asaphid, two pairs of large spines are present, whereas there are three pairs in the remopleuridid. At first glance the anterior and posterior pairs in both groups appear to be homologous and the intermediate pair (fixigenals) a characteristic of the remopleuridid alone; but I believe this is not the case. I think it is more probable that the posterior spines in the asaphid are the fixigenals and that the posterior pair in the remopleuridid (belonging to the protopygidium) appeared at a stage later than that represented in my asaphid material. This seems a reasonable hypothesis for two reasons. First, in protaspides of both families the spines I interpret as fixigenal show the same spatial relationship with the points where the posterior branches of the facial sutures cut the doublure (indicated by the arrows in text-figs. 4,5). Second, evidence discussed earlier points to marked differential growth of the protopygidium in the posterior median area after the stage represented by the asaphid forms illustrated here. It seems more reasonable that (a) the developing protopygidium expanded to the free margin along the midline by displacing toward the right and left the fixigenal spines (together with the ends of the free cheeks) than that (b) the posterior spines separated only slightly while the closely adjacent ends of the free cheeks spread wide apart in accommodating the margin of the protopygidium. These alternatives are shown diagramatically in text-fig. 6.

If my interpretation is correct, then the first protopygidial segments began to develop in an area immediately behind the part of the cranidium that became the occipital ring. At first only the axial portions of the new segments appeared. At that time the site of segment addition was completely surrounded by portions of the cranidium. As the new segments developed further, differential growth forced the genal angles apart, allowing the expanding protopygidium to reach the free margin.

At least two factors may be reflected by differences between the early ontogenies of trilobites like those noted in the preceding discussion. First, mineralization of the exoskeleton may have begun at an earlier or later developmental stage depending on the genus, or possibly related to the ecology of the young stages. Second, the rate of development of one part of the protaspis relative to another may have varied from one group of trilobites to another. Although these

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EXPLANATION OF PLATE 117

FIGS. *1–4*—Earliest protaspis found. Still attached but incomplete ventral plate includes free cheeks and hypostome unseparated by sutures. Dorsal, anterior, ventral and oblique ventral views. USNM 138800; locality 1. ×30.

5–8—Intermediate protaspid stage. Four successive exterior views taken as the specimen was rotated forward about a transverse axis. USNM 138805a; locality 4. ×25. Same specimen in lateral view on pl. 118, fig. 2.

9–12—One of latest protaspid stages found. Views as in figs. 5–8. USNM 138805b; locality 4. ×25. Equivalent stage in lateral view on pl. 118, fig. 4.

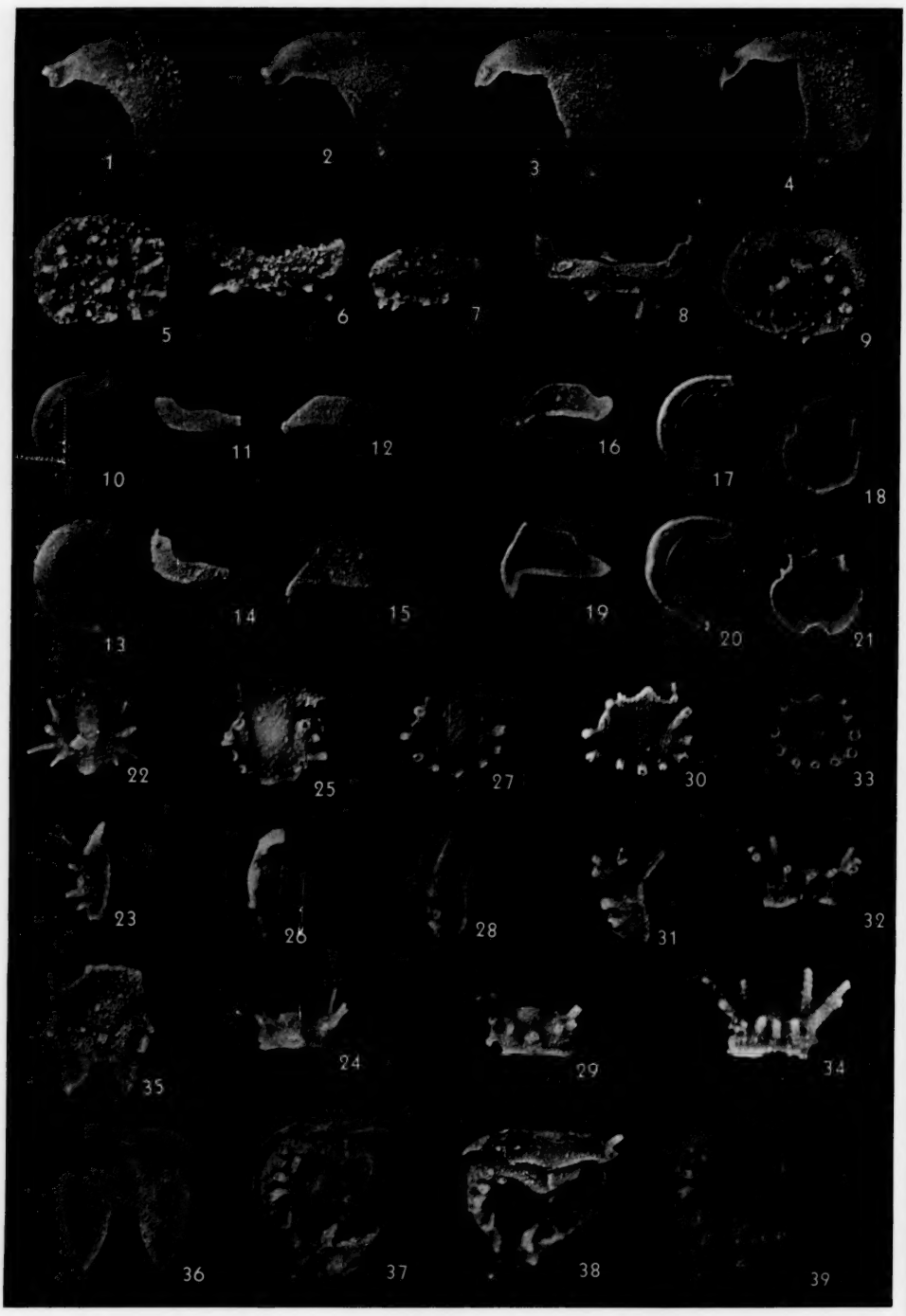
13,14—Interior and oblique views of protaspis slightly more advanced than figs. 1–4. USNM 138802a; locality 3. ×25. Same specimen as pl. 118, fig. 1.

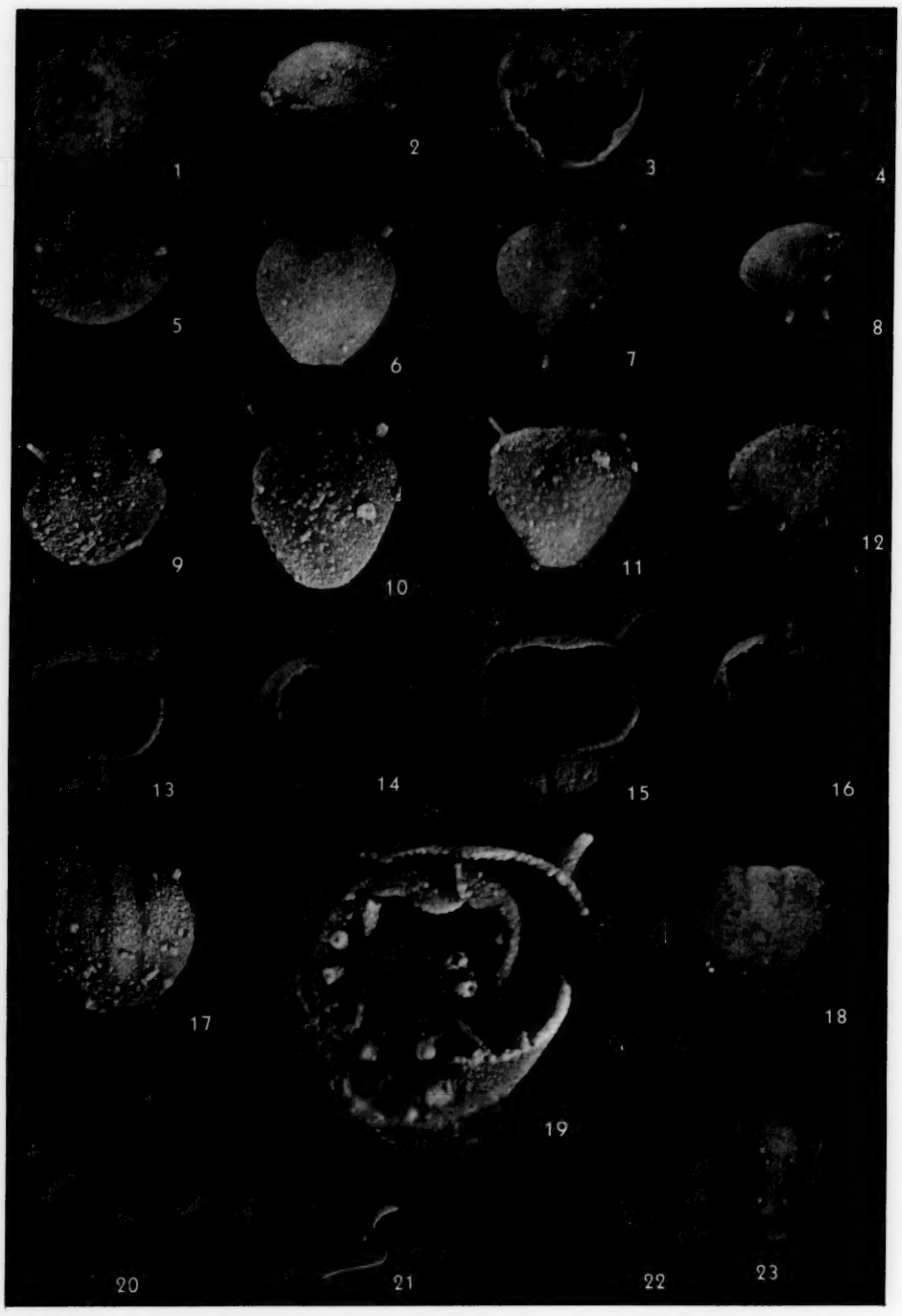
15,16—Interior and oblique view of protaspis about comparable to figs. 9–12. Note short forked process at posterior midline of inner margin which separated ends of free cheeks. USNM 138802b; locality 3. ×25. Same specimen as pl. 118, fig. 4.

17,18—Exterior views of two protaspides of a species in which axial furrows of cranidial region are long and distinct. Both specimens represent about same level of development as figs. 9–12. *17*, direction of view intermediate between figs. 9 and 10. USNM 138810a. *18*, direction of view intermediate between figs. 10 and 11; note traces of protopygidial segmentation on axis and left flank of posterior portion. USNM 138810b. Both from locality 10a. ×25.

19—Approximately ventral view of a complete protaspis in which the two free cheeks and hypostome are slightly displaced from their natural position. Stage of development like figs. 9–12. USNM 138803; locality 3. ×45.

20–23—Dorsal and anterior views of two early meraspid cranidia representing two different asaphid species (or possibly genera). *20,21*, probably the same species as figs. 5–16; USNM 138804; locality 4. *22,23*, probably the same species as figs. 17 and 18; USNM 138809; locality 10a. All ×12.5.





factors may account for some of the observations made on asaphid and remopleuridid protaspides, they do not contribute to an understanding of the gap in the record of asaphid development. This gap, I believe, is real, but it remains to be explained.

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EXPLANATION OF PLATE 118

FIGS. *1–4*—Left lateral views of four progressively more advanced protaspides. Three of same specimens also figured on pl. 117. *1*, USNM 138802a; locality 3. *2*, USNM 138805a; locality 4. *3*, USNM 138802c; locality 3. *4*, USNM 138802b; locality 3. All ×25.

5–7—Ventral plate from an early protaspis (probably about the same stage as pl. 117, figs. 1–4) in which hypostome and free cheeks form a single unit. Ventral, anterior and left lateral views. USNM 138805c; locality 4. ×30.

8,9—Free cheeks and hypostome from a more advanced protaspis, separated by sutures but still adhering to each other. Anterior and ventral views. USNM 138805d; locality 4. ×25.

10–15—Two right free cheeks in ventral, anterior and right lateral views, *10–12*, intermediate level of development; compare course of facial suture with fig. 2. USNM 138806*a*. *13–15*, from more advanced protaspis; compare suture with fig. 4. USNM 138806b. Both from locality 4. ×25.

16–21—Two left free cheeks in interior-lateral and dorsal views, and two hypostomes in interior-dorsal view. Cheeks (×25) represent about same two developmental stages as figs. 10–15; hypostomes (×30) approximately match cheek stages, except fig. 18 is before development of ventral sutures. *16,17*, free cheek; hypostomal suture corresponds to tripartite suture of fig. 27. USNM 138806c. *18*, hypostome. USNM 138807a; same specimen as figs. 22–24. *19,20*, free cheek; hypostomal suture corresponds to bipartite structure of figs. 21 and 30. USNM 138806d. *21*, hypostome. USNM 138807b; same specimen as fig. 33. All from locality 4.

22–34—Progressive series of hypostomes in ventral, left lateral and posterior views. *22–24*, stage before development of median and hypostomal sutures; free cheeks broken off. USNM 138807a. *25,26*, slightly later stage; ventral sutures still not developed; cheeks broken. USNM 138807c. *27–29*, hypostomal suture well formed, tripartite. USNM 138807d. *30–32*, hypostomal suture bipartite; anterior wing long. USNM 138808a. *33*, specimen whose broken spines expose deep median notch in posterior margin. USNM 138807b. *34*, specimen with long, well-formed spines. USNM 138808b. All from locality 4. ×30. Note especially the progressive development of: hypostomal suture, anterior wing, median posterior tubercle-spine, median posterior notch, dorsoventral dimension of lateral surface, thickening along free dorsal margin.

35,36—Two hypostomes in exterior view. *35*, meraspid specimen. USNM 138810c; locality 10a. ×30. *36*, holaspid specimen. USNM 138801; locality 1. ×5.

37,38—Protaspis with free cheeks and hypostome; same specimen as pl. 117, fig. 19. Ventral stereograph and anterior view. USNM 138803; locality 4. ×25.